ASSESSING THE ROLE OF WOODY COVER IN RESOURCE SELECTION BY SABLE ANTELOPE (*HIPPOTRAGUS NIGER*) IN NORTHERN KRUGER NATIONAL PARK

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A research report submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in partial fulfilment of the requirements for the degree of Master of Science

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DECLARATION

I declare that this thesis is my own unaided work. It is being submitted for the Master of Science by coursework and research report at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any other degree or examination in any other university.

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ABSTRACT

The relationships between woody cover and habitat use by sable antelope (*Hippotragus niger*) in Kruger National Park (KNP) are poorly documented. Previous studies of sable antelope habitat did not explicitly measure space use and its relationship to habitats attributes. Global positioning system (GPS) telemetry permits the accurate collection of animal locations, which can be used to estimate home ranges and utilisation distributions (UDs). Resource utilisation functions (*i.e.*, functions regressing probabilistic space use by animals such as UDs on landscape attributes) were used to analyse relationships between habitat use and woody cover with historical black and white aerial photographs. The dot-grid and object-based image analysis (OBIA) methods were used to estimate woody cover from digital aerial photographs and the results validated with field collected woody cover data. The dot-grid method was used to estimate woody cover by expressing canopy hits as a percentage of total dots using a regular lattice of evenly spaced dots overlaid on digital aerial photograph sections. The OBIA approach selected homogeneous groups of pixels (*i.e.*, objects) and incorporated image aspects such as shape, size, texture, and brightness into the woody cover classification. The size of the objects depended on the scale selected for identifying single woody plants and the resolution of the aerial images. The two woody cover estimators (*i.e.*, the dot-grid and object-based image segmentation) produced contrasting results. However, more confidence was placed in the use of the dot-grid method. The linear regression models revealed weak/ non-significant relationships between woody cover and space use by sable antelope. However, woody cover was more abundant in the wet season home range (36 ± 1%) when

compared with the dry season home range (30 ± 1%) ($t_{0.05, 163} = 3.8$, $P < 0.001$). Woody cover in the dry season non-core areas (31 ± 1%) was significantly more than that in the core areas (28 ± 1%) ($t_{0.05, 182} = -1.7$, $P = 0.04$). The avoidance of home range areas with more woody cover during the dry season suggests that sable antelope are risk sensitive foragers that maximise the intake of available low quality food resources. The results from this study also indicate that sable antelope may be selecting for woody cover at scales larger than the one used here.

For my parents

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CHAPTER ONE

1.1 Introduction to Study

Sable antelope (*Hippotragus niger*) populations have undergone a severe decline in KNP (Harrington, 1995; Owen-Smith *et al*., 2005; Von Richter, 1974; Wilson and Hirst, 1977). Many reasons have been suggested to explain the decline: habitat deterioration (Harrington, 1995), predation (Owen-Smith and Mills, 2006), climatic variation (Ogutu and Owen-Smith, 2005) and competition with other grazers (Harrington *et al*., 1999). However, there are no studies explicitly relating sable antelope habitat use to vegetation structure, which is a responsive habitat element to climatic and topographic variation.

Vegetation structure is also an important landscape and habitat element for herbivores as it forms the functional backbone of many ecosystems (Halls, 1973; Pickett and Cadenasso, 1995; Mysterud and Ostbyte, 1999; Shachak *et al*., 2008). The use of woody cover by animals varies between seasons in response to phenology, climate, food abundance (Grobler, 1981; Kutilek, 1979; Mysterud and Ostbyte, 1999), and predation risk (Lima, 1998; Riginos and Grace, 2008; Schooley *et al.*, 1996). New predictive models capable of untangling habitat use patterns are already being used in animal ecology (Manly *et al.*, 2002). Geographic information systems (GIS) provide opportunities for analyzing animal-landscape interactions, and may provide useful spatial information on habitat use patterns necessary for the conservation and management of threatened populations (Guisan and Zimmerman, 2000; Manly *et al.*, 2002). The availability

of GPS telemetry data from sable antelope and historical aerial photographs presented an opportunity for analyzing herbivore-vegetation interactions. Probabilistic measures of space use have not been used to relate habitat use by sable antelope from GPS collars to woody cover abundance. The goal of this study was to bridging the space use gap and describe seasonal variation in habitat use patterns.

1.2 Aim

To assess relationships between woody cover and seasonal habitat use patterns by sable antelope (*Hippotragus niger*) in northern KNP using resource utilisation functions.

1.3 Objectives

1) Compare relationships between woody cover and seasonal habitat use by sable antelope at different seasons using RUFs,
2) Compare mean woody cover in home range isolines within and between seasonal UDs.

1.4 Hypotheses

1.4.1 Hypothesis for testing objective 1

H_0: Sable antelope use areas within their home range indiscriminate of woody cover abundance.

H_{1A}: During the wet season, sable antelope use foraging areas within their home range in direct proportion to woody cover abundance.

H_{1B}: During the dry season, sable antelope use foraging areas within their home range in inverse proportion to the abundance of woody cover.

1.4.2 Hypotheses for testing objective 2

1.4.2.1 Hypothesis for testing objective 2 within home range use areas

H_0: Sable antelope do not distinguish between woody cover occurring in home range use areas.

H_1: Sable antelope frequently forage in areas with less woody cover in their home ranges use areas.

1.4.2.2 Hypothesis for testing objective 2 between seasonal use areas

H_0: Sable antelope use areas with the similar woody cover characteristics during the wet and dry seasons.

H_1: Sable antelope use areas with more woody cover during the wet season compared with the dry season

1.5 Literature Review

The sable antelope (*Hippotragus niger*) population in the KNP declined from approximately 1100 individuals (Von Richter, 1974), to approximately 450 individuals distributed throughout the park (Prof. Norman Owen-Smith, personal communication). There is concern that declines in sable antelope populations and that of other rare antelope (*e.g.*, roan antelope [*Hippotragus equinus*]) in KNP may be the result of poor habitat conditions (Harrington *et al.*, 1999). Vegetation composition and structure forms the foundation of an animal's habitats and consequently affects the distribution and habitat use patterns of herbivores (Senft *et al.*, 1987). A current global threat is climate change caused by increased amounts of green house gas emissions into the atmosphere (*e.g.*, carbon dioxide), and fears are that this may favour woody plants in contrast to grass species (Johnson *et al.*, 1993). Eckhardt *et al.* (2000) reported that woody cover in the northern plains of KNP, where most of the rare antelope live, had increased by 12% during the period 1940-1998. Woody cover has the potential to affect the distribution of ungulates such as sable antelope in future climate change scenarios. Sable antelope are specialist grazers favouring environments with adequate food quality and quantity, which may be characterised by the abundance of grass (Estes and Estes, 1974). Other habitat requirements for ungulates include water, adequate cover for protection from weather, and concealment cover from predators (Mangel and Clarke, 1986; Mysterud and Ostbyte, 1999), and for mating and rearing of young (Block and Brennan, 1993). The landscape configuration and density of woody plants is important as it affects aspects of animal ecology already mentioned.

1.5.1 Woody Cover and its Quantification

Woody cover is composed primarily of above animal (canopy cover) and ground cover that obstructs viewing from lateral positions (Mysterud and Ostbyte, 1999; Figure 1.1). Microclimates for ungulates can be affected by the presence of vegetation cover through the lowering body temperatures on hot days (*e.g.*, moose (*Alces alces*) (Belovsky, 1981)). Other effects of woody cover are on hydrology (*e.g.*, water retention and distribution [Archer, 1997, Medina and Silva, 1990]), and grass abundance (*i.e.*, trees compete with grass for space and mineral resources (Scholes and Archer, 1993)). Woody cover is not a static component in landscape as factors affecting plant growth (*e.g.*, soil nutrients, fire, herbivory, soil moisture) can cause variation in woody cover (Sankaran *et al.*, 2004).

Woody cover in African savannas changes in response to biotic and abiotic factors. Increased stocking rates of wild and domestic ungulates can cause bush encroachment (Molele *et al.*, 2002), thus increasing woody cover abundance at the expense of grass cover. This situation favours increases in browsing communities but reduces grazers. However, woody species abundance has been shown to improve grass quality (*i.e.*, high leaf/stem ratio, high nitrogen content and low fibre concentrations) for herbivores (Gordon *et al.*, 2008; Ludwig *et al.*, 2008). Wildebeest (*Connochaetes taurinus*) in the Tarangire National Park, Tanzania, preferred grazing under tall *Acacia tortilis* trees where the grass nutrient quality was high (Ludwig *et al.*, 2008). Gordon *et al.* (2008) suggest that in future climate change scenarios in savannas where woody species are expected to increase because of CO_2 loading in the atmosphere, that grass quality may decline thus limiting grazers. Trees are efficient in using water and nutrients in the presence of

high atmospheric CO_2 (Johnson *et al.*, 1993). However, there are also factors that lead to negative changes in woody cover such as land use changes (Gordon *et al.*, 2008) and damage by elephants (*Loxodonta africana*) (Eckhardt *et al.*, 2000; Tafangenyasha, 1997).

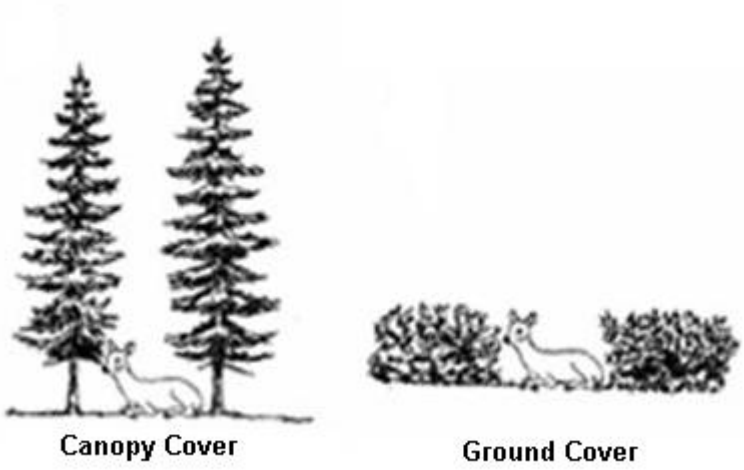


Figure 1.1: Vegetation cover types with respect to ungulates
Source: Mysterud and Ostbyte (1999)

Woody cover not only affects the food available to grazers but may also increase their susceptibility to predation. Schooley *et al.* (1996) reported that the presence of shrub cover increased predation rates of Townsend's ground squirrels (*Spermophilus townsendii*). In ungulates, shrub cover and tree trunks can obscure lateral vision, particularly during feeding and this can increase predation risk in the absence of vigilant behaviour (Jarman, 1974; Lima, 1998), and obstruct prey escape routes. Mysterud and Ims (1998) suggested that grazers assess associated

risks between feeding and predation, and are faced with trade-off situations (*i.e.*, safety versus nutritional gain). Elk (*Cervus elaphus*) in Yellowstone National Park in the United States avoided areas with high vegetation cover after the reintroduction of grey wolves (*Canis lupus*) (Mao *et al.*, 2005). Funston *et al.* (1998) found that male lions (*Panthera leo*) successfully hunted in savanna woodlands in the KNP where they are less conspicuous to high prey densities of impala (*Aepyceros melampus*) and African buffalo. However, male lions depended on female hunts in open areas. Much of the sable antelope habitat is in the woodland savanna biome (Skinner *et al.*, 2005). Woody cover is sometimes characterised by variability and patchiness at landscape and patch levels (Venter *et al.*, 2003). The landscape is heterogeneous because of variable interactions among factors affecting plant growth in savanna biomes (Rogers, 2003). However, factors leading to vegetation patterns will not be discussed but only their contribution to habitat use patterns.

The hierarchical structure in landscape patterns is caused by functional heterogeneity occurring at different scales (Legendre, 1993; Kotliar and Wiens, 1990). Although plants usually have clumped distributions, small-scale and large-scale heterogeneity affects species composition, vegetation structure, tree and shrub distribution and subsequently woody cover (Levick, 2008; Venter *et al.*, 2003). According to the hierarchical patch dynamics paradigm, ecosystems are structured in a series of vertical organisational levels that are constrained within nested structures (O'Neill *et al.*, 1986). Higher levels of structuring have low functional process rates and occur at broad scales and they also constrain lower levels that have faster process rates because of the finer scales (spatial and

temporal) which they occur (Allen and Starr, 1982; Kotliar and Wiens, 1990). Woody cover is therefore not expected to change significantly at large temporal scales in the absence of disturbances in temperate and equatorial latitudes; the only difference is that some trees shed their leaves in response to environmental conditions. Problems can arise in the use of aerial photographs when photos are taken at inappropriate times, particularly for deciduous trees and when the photos are old because they may present problems when inventorying young forests or areas with accelerated land-use changes. However, because of the slow process rates, some aerial photographs taken within a single year can be used in forest inventories with less marginal error, especially in temperate and evergreen forests.

Functional process rates and spatial structuring criteria are used to define patches, which form the boundaries of organization levels (Pickett and Cadenasso, 1995). Patches differ from their surroundings but are assumed internally homogeneous (Kotliar and Wiens, 1990). Since woody vegetation cover is patchy in nature, its measurement must depend on an appropriate sampling scale. Mitchell *et al.* (1988) observed that woody cover estimates depended on the sizes of plots used. They also reported that woody canopy cover was overestimated in low cover areas, whilst it was underestimated in high cover areas. Vegetation structure at landscape scale is considered to be stable but with frequent changes, occurring at fine scales (Archer, 1997; Bormann and Likens, 1979). This situation presents some difficulty in the temporal classification and mapping accuracy of landscape-level woody cover using airborne sensors [*e.g.*, satellites and airplanes] (Lillesand and Kiefer, 1994).

Mapping woody cover using airborne sensors allows large areas to be sampled at relatively low costs with minor disturbance to tree and animal life (Paine, 1981; Russ, 1999). Black and white aerial photography has been extensively used for vegetation mapping in forestry, agriculture, and wildlife studies due to its low cost, historical availability, accuracy, and stereoscopic capabilities (Fensham *et al.*, 2002; Paine, 1981; Figure 1.2). Digitisation of photographs has enabled the advance of vegetation science, as landscape-level inventories can be easily conducted using powerful computers (Lillesand and Kiefer, 1994). Woody cover is one of many habitat attributes whose abundance can be estimated from aerial photographs as it is unbiased by size and distribution of individuals (Floyd and Anderson, 1987). Several methods are available for estimating cover from aerial photos: visual estimates, dot-grid, line-intercept or transect method and digital image analyses (Nowak *et al*., 1996). The training of image classifiers and validation of supervised classification depends on representation, sample size and distribution of vegetation units (Muchoney and Strahler, 2002).

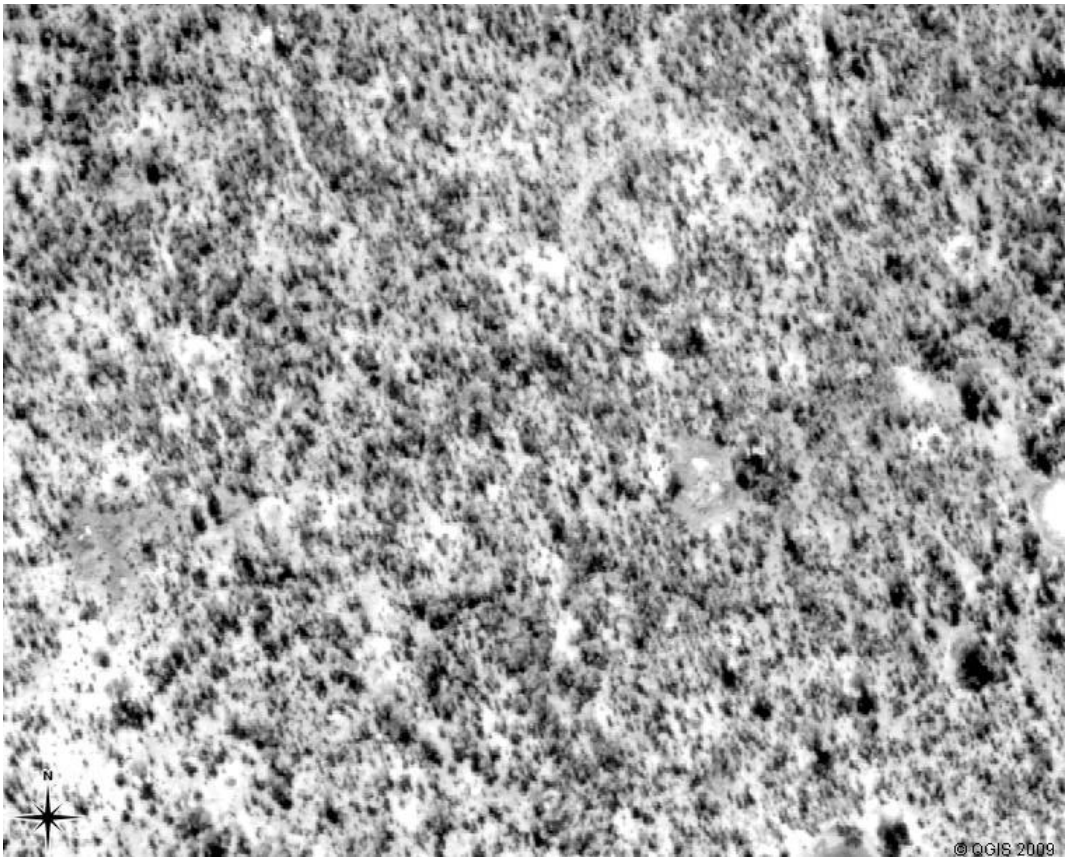


Figure 1.2: Black and white aerial photograph of a section of Punda Maria in 2004 with ~32% woody cover.

Traditional aerial photo interpretation of woody cover depends on human observers. These manual methods are often fast and cheap but are subjective (Paine, 1981). Examples of manual methods include the dot-grid and aerial line-intercept. Advancement in environmental information technology has resulted in faster automated processing for digital image analyses. The pixel-based classification approach using only the spectral properties of features in digital images is a common approach (*e.g.*, the maximum likelihood classifier (Carmel and Kadmon, 1998; Russ, 1999)). However, this approach performs poorly in savannas because of landscape heterogeneity and seasonal phenology. The

comparisons of aerial woody cover maps to ground data fail because of non-stationarity that causes non-linear relationships because of uneven variance, which is a result of non-random spatial distribution of variables of interest (Moran, 1950; Rosema *et al.,* 1992). Field measurements often do not correlate well with digital image classifications and this is problematic when developing simple linear interpolation models that reduce forest inventory time. It is difficult to select enough training pixels in images of heterogeneous landscapes and this affects image classification results (Lu and Weng, 2007). Landscape level heterogeneity also violates the assumption of normal spectral distribution of features (*e.g.*, tree crowns). Coarse resolution black and white photographs may further compound the problem as there is an increased probability of spectral signature overlap among features (*e.g.*, between trees and shrubs). The lack of a unique signature thus reduces classification accuracy (Carmel and Kadmon, 1998; Lu and Weng, 2007; Russ, 1999). The use of object-based image classifiers that incorporate texture, height, size, and shape of objects improves overall classification performance (Laliberte *et al.*, 2004). Manual methods such as the dot-grid method, a measure of shrub and tree canopy hits from a regular lattice of dots, are still considered accurate (Mapaure and Campbell, 2002; Randolph, 2004), although their objectivity has been criticised (Dublin, 1991).

The success of classification algorithms depends upon their agreement with ground data. Field-based methods for measuring woody cover at plot scales include the spherical densiometer (Lemmon, 1956), line intercept, ocular estimates and digital photography (Korhonen *et al.*, 2006). Korhonen *et al.* (2006) found that labour intensive methods such as the line-intercept and cajanus tube

gave good woody cover estimates while other methods improved with increases in plot numbers. The fundamental question is *how well do field and remotely sensed data agree?* Fensham *et al*. (2002) found problems when relating remotely sensed data to field measurements using direct linear relationships such as linear regression as both measures are subject to errors of unknown magnitude. The situation is amplified by spatial dependencies in data, which automatically induces spatial autocorrelation in woody cover. However, this can be addressed by using non-linear techniques such as *kriging* (Dungan *et al*., 1994; Laslett, 1994; Wei and Chen, 2004). *Kriging* is a geostatistical method used when spatial data is collected at limited locations such that estimates of values from *unsampled* locations can be extrapolated (Laslett, 1994). Precise quantification of woody cover provides a useful input into habitat use and selection studies.

1.5.2 Quantifying Habitat Use and Selection

In addition to quantifying woody cover, the actual space used by animals has to be measured so that preferential use can be identified. Block and Brennan (1993) defined habitats as the complement of physical and environmental conditions favouring the occupation of space by individuals. Traditional methods of measuring habitat use focused on "used" and "available areas" and thus classification was based on presence-absence data (Hirzel *et al.*, 2002; Johnson, 1980; Neu *et al.*, 1974; Thomas and Taylor, 1990). These methods are inadequate because "availability" of areas relative to animals is arbitrarily defined and may not represent the actual areas "available" to animals (Aebischer *et al.*, 1993; Hall *et al.*, 1997; Manly *et al.*, 2002). Some researchers have gone around the problem by solely focusing on used areas (*e.g.*, Traill and Bigalke, 2006). In addition, sampling has often been carried out at inappropriate scales (*i.e.*, locations independent of individuals instead of *vice-versa* (Magome, 1991; Neu *et al.*, 1974)). This often arises from pooled observations of animal locations (or observations), which violates the statistical assumption of independence whereas individuals should be identified and sampled instead (Aebischer *et al.*, 1993). Hall *et al*. (1997) therefore cautioned against the use of the term "availability" with respect to habitats, as it cannot be quantified easily. They proposed that "abundance" be used instead. Animals may not frequent all areas in their habitats within the temporal scales used in most studies (Bailey *et al.*, 1996). Some studies have been designed to account for this by sampling continuously or seasonally (Anderson *et al.*, 2005; Erickson *et al.*, 1998; Lombardi *et al.*, 2007).

However, the problem of adequately defining use still persists as species absence does not imply animals never use an area. MacKenzie *et al*. (2002) proposed a likelihood-based approach to circumvent this by measuring probability of use (site-occupancy) as a function of the probability of presence of an animal at a site and the detection probability during a sampling period using presence-absence data. Although this method uses presence-absence data, it is a more robust resource selection function (RSF) in that covariates ("static" landscape attributes) can be included in the model (MacKenzie *et al*., 2002; MacKenzie *et al*., 2003). The site-occupancy method is robust to missing observations as detection probabilities are a function of frequency of detection and are site independent. An *a priori* assumption or estimation of the presence of a species at sites is necessary for the model to work. However, for the sable antelope, this data was not present and the only way to obtain this at the least cost was to use estimate a probability of use surface using GPS telemetry data. For this reason, the site-occupancy model was not used but its integration in subsequent studies (after probability of presence/ use has been estimated), will enhance the accuracy and usefulness of future sable antelope studies. The other drawback in using the site occupancy model may be the potential effect of spatial heterogeneity on food resource and subsequently detection and presence probabilities (MacKenzie *et al*., 2002). This is likely to be a problem, especially in the KNP savanna.

The increased volume of accurate animal locations from GPS telemetry studies, analyses of these data have invalidated some traditional "used-available" and "presence-absence" studies, as actual use of resources by animals can be approximated (Aebischer *et al.*, 1993; Kernohan *et al.*, 2001; Manly *et al.*, 2002).

Habitat use by animals in landscapes is not discrete; it can be either continuous or discontinuous in response to landscape patchiness and environmental gradients (Kotliar and Wiens, 1990; Legendre, 1993; Senft *et al*., 1987). Home ranges (*i.e.*, areas individuals use for their normal life activities) are represented in two-dimensional space (Burt, 1943). There are many other home range estimators: kernels, fractal estimates, UDs, centre of activity, minimum convex polygons, and mechanistic home range methods among others (Powell, 2000). Kernel home ranges are recommended in home range literature because they give good home range estimates and can be used to generate UDs (Kernohan *et al.*, 2001). Utilisation distributions model a continuous probability surface of space use (*i.e.*, a probability density function) by individual animals and overcome problems relating to independence of animal location estimates (Marzluff *et al.*, 2004; Worton, 1989). However, the alternative site-occupancy models are robust and fully satisfy the assumptions of independence (MacKenzie *et al*., 2002). The difference between kernel home ranges and UDs is that the former are two dimensional, while the latter are three-dimensional. Utilisation distributions give a probability of use at specific locations (x, y), which is equivalent to density function (Figure 1.3). Unlike site-occupancy models which are a gross characterisation of the probability of presence/ space use, UDs assume that space use has been precisely measured. The advantage of fixed kernel UDs is that they model space use as a continuous variable in the landscapes (Silverman, 1986; Worton, 1989). Formally, the function is:

$$\text{UD} = [\, \hat{f}_{\text{UD}}(x,y) \text{ at location } (x, y), \text{ where } \; x, \; y \in \mathbb{R} \,] \qquad (1.1)$$

Function 1.1 is translatable into a three dimensional kernel density surface (*e.g.*, Figure 1.3).

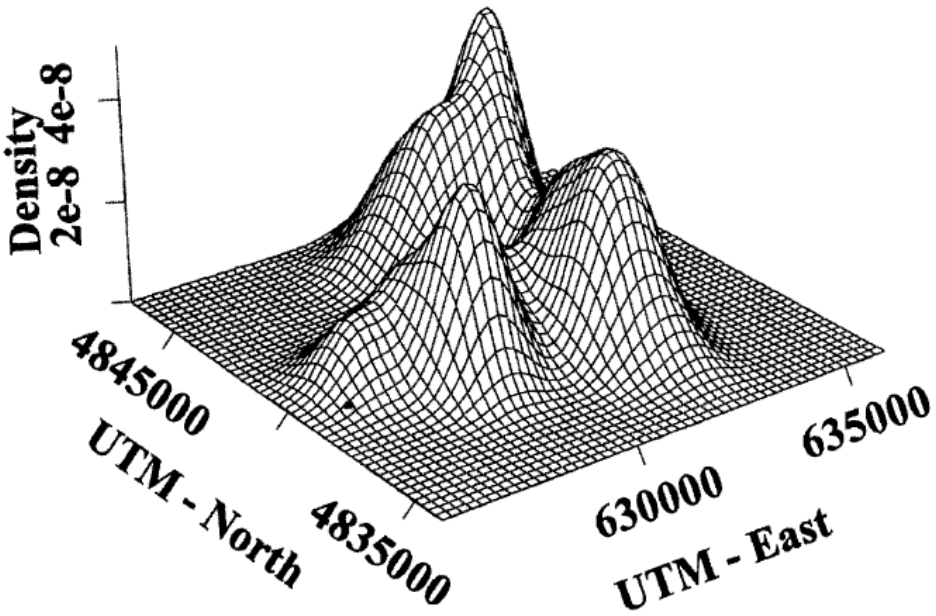


Figure 1.2: Kernel density surface *[adapted from Gitzen and Millspaugh (2003)]*

Home ranges represent the highest level of selection of broad landscape features by animals (Johnson, 1980; Senft *et al.*, 1987). Herbivore home ranges are located in areas with adequate water, food and cover (Senft *et al.*, 1987), and this may explain their large spatial extent. Home range estimates using non-parametric kernelling procedures are popular in animal ecology because they make no assumptions about the statistical distribution of location estimates (Kernohan *et al.*, 2001; Hemson *et al.*, 2005). Animal movements are rarely

random (Pyke, 1978), although some foraging bouts approximate randomness (Bailey *et al.*, 1996). Bailey *et al.* (1996) posited cognitive spatial memory, which is a function of reward-loss arising from experiential use of particular areas as a factor determining non-random space use by herbivores in response to clumped resources.

The shapes of kernel density estimators are affected by the choice of a smoothing parameter/ bandwidth (Kernohan *et al.*, 2001; Seaman *et al.*, 1999; Worton, 1989). There are two types of kernels: adaptive and fixed, and several smoothing parameters that are used (Silverman, 1986). Fixed kernels use the same bandwidth to smooth all observations, while adaptive kernels use variable smoothing with less smoothing for clumped locations and greater smoothing for dispersed locations (Worton, 1989). Fixed kernel home ranges using the least-squares cross-validation (LSCV) smoothing parameter are considered reliable home range estimators (Kernohan *et al.*, 2001; Seaman and Powell, 1996). Optimal smoothing of the home ranges was achieved with a raster resolution of 50 m. However, Hemson *et al.* (2005) cast doubt upon this "one-size-fits-all" approach by showing its inadequacy in estimating the home range of lions (*Panthera leo*) in Botswana. The standard method was inconsistent (*i.e.*, had more failure rates) in the estimation of home ranges of animals with high site fidelity, numerous locations, and variable small sample size of locations. Horne and Garton (2006) proposed the use of the likelihood cross-validation (LCV) smoothing parameter instead because it produced better model fits with less variability using fixed kernels. Gitzen and Millspaugh (2003) had earlier raised concerns over the LSCV bandwidth's reliability due to inconsistency (and

variability) in home range estimates in available software. Current studies advocate the use of plug-in methods or "solve-the-equation" in which the smoothing parameter is specifically calculated (Gitzen and Millspaugh, 2003; Millspaugh *et al.,* 2006). Getz *et al.* (2007) developed a more robust kernel method for measuring home ranges and utilisation distributions, which is a hybrid of minimum convex polygons, and kernel methods called localised convex hull method (LoCoH). However, much software expertise is needed when using this method compared to kernels (*e.g.,* calculation of appropriate smoothing parameter). The result is that kernel methods are still in popular use because of their versatility.

Habitat selection by animals can be measured using many statistical tools, among them, RUFs. A detailed discussion of resource selection functions in Manly *et al.* (2002). Resource utilisation functions improve upon the Manly *et al.* (2002) resource selection functions in that they measure habitat use as a continuous variable compared to the discrete measurement in the latter. Resource utilisation functions are generated from regressing local and landscape level resources on an individual's utilisation distributions in a spatially explicit way (Hepinstall *et al.,* 2003). The proportion of time spent by herbivores in areas within their home range is a linear function of the abundance of particular resource of interest (*e.g.*, woody cover in this case; Senft *et al.,* 1987). Stochastic dynamic programming models used by Newman *et al.* (1995) suggested linear relationships existed between habitat use and resource abundance. However, spatial autocorrelation is induced in studies using RUFs, as the assumption of independence among UD grids / pixels is violated (Hepinstall *et al.,* 2003). In

addition, non-stationarity and spatial autocorrelation is associated with the landscape attributes such as the abundance of woody plants in heterogeneous environments (Rosema *et al.*, 1992; Schabenberger and Gotway, 2005), affecting habitat selection models.

1.5.3 Factors Affecting Habitat Selection by Ungulates

Precise quantification of space use enables ecologists to measure species habitat attributes so that they can infer behaviour such as habitat selection. Johnson (1980) described habitat selection as the disproportionate use of habitat resources and Block and Brennan (1993) mention that it is scale dependent. There are many factors which can influence resource selection by ungulates including predation risk (Riginos and Grace, 2008), food availability (Senft *et al.*, 1987), water availability (Redfern *et al.*, 2003) and season and leaf phenology (Wilson and Hirst, 1977). Predators have direct effects on prey populations through lethal consumption and non-lethal effects on prey. Lima (1998) suggested that non-lethal effects of predators on prey have larger ecological impacts than actual predation. Elk (*Cervus elaphus*) in the Greater Yellowstone Ecosystem adjusted herd sizes and habitat use in response to predation risk from grey wolves (*Canis lupus*) (Creel and Winnie, 2005). Elk herd sizes were smaller when wolf predation was high and open areas and roads were avoided. DelPerno *et al.* (2003) Krausman that predator avoidance was gender related in white-tailed deer (*Odocoileus virginianus dakotensis*). Males had lower risks of predation due to large body sizes and therefore did not select for woody cover compared to females

and maternal herds that selected for woody cover. Females chose areas with more protective cover during the summer when they had fawns but in winter when food was limiting, they chose areas with less cover.

Riginos and Grace (2008) reported that in *Acacia tortilis* dominated savanna woodlands of Kenya that wild herbivores chose open areas in direct response to predator presence. Increased vigilance, alteration of group sizes and differential use of cover are common responses by prey in response to the presence of predators (Hirth, 1977; Jarman, 1974; Lima, 1998; Riginos and Grace, 2008). Predation risk alters herbivore behaviour such that they use marginal sites/ patches were food quantity and quality is low (Houston *et al.*, 1993). Lima (1998) suggested that animals reduce activity cycles (*i.e.*, seeking refuges and increasing vigilance) as a predator avoidance strategy so that they minimise the probability of encountering predators. However, there is no overwhelming evidence linking predation as a limiting factor in populations of African ungulates and suggestions are that drought mediated food scarcity is responsible (Mduma *et al.*, 1999; Owen-Smith *et al.*, 2005; Rettie and Messier, 2000).

Food is a fundamental requirement for all living organisms. It is not surprising that herbivores choose habitats in areas with abundant food resources that can meet their body maintenance requirements (Senft *et al.*, 1987). Some animal species secure food resources and defend them from other animals thus establishing territories. When food resources are abundant and uniformly distributed in space, most animals will not exhibit any form of selection and therefore aggressive behaviour is minimised (Houston *et al.*, 1993). This ideal situation is not present in nature as food resources such as foraging grass are

patchily distributed, while their abundance may be limited by environmental factors such as water and nutrient availability. Woody cover can change grass productivity and cover which are essential components in grazing ecosystems (Gordon and Prins, 2008; Ludwig *et al.*, 2008). Treydte *et al.* (2007) found that shade-tolerant nutritious grass (*Panicum maximum*) growing under tree canopies had 25% more nitrogen than grasses in the open, and hence serves to attract herbivores. Changes in food abundance and quality directly affect grazing herbivores, which causes herbivores to change their behaviour to meet their food requirements.

Molvar and Bowyer (1994) observed an increase in aggressive behaviour in larger Alaskan moose (*Alces alces gigas*) herds compared with smaller ones because of direct intra-specific competition for resources (*e.g.*, food) when woody cover was abundant. There are seasonal differences in the response of herbivores to woody cover. Female white-tailed deer used areas with low woody cover during winter when food resources were scarce compared to areas with more cover during the summer (DelPerno *et al.*, 2003). Grobler (1981) observed sable antelope using more open savanna woodlands during the dry season compared with the areas used during the wet season. However, the presence of tall trees and/ or shrubs is known to improve the quality of grass (Jackson and Ash, 1998; Ludwig *et al.*, 2008). Wildebeest in Tarangire National Park were found to prefer grazing in areas under *Acacia* tree canopies and dead tree stumps when compared to open grasslands (Ludwig *et al.*, 2008). Herbivores in temperate latitudes where tall forest are common, used areas with more cover (Hirth, 1977) when compared with savanna herbivores, which use open areas (Riginos and Grace, 2008).

However, animals are faced with a trade-off between predation risk and active foraging (Brown, 1999; Mysterud and Ims, 1998; Riginos and Grace, 2008), and thus it is difficult to separate these two behavioural responses. For example, increased vigilance is inversely related to the amount of time spent foraging, although it is generally assumed that animals learn to optimise their behaviour accordingly (Houston *et al.*, 2003).

Autocorrelation occurs when observations from a variable are related to each other and the two types are serial autocorrelation and spatial autocorrelation with the former time dependent and the latter deal with the relationships of locations in space (Legendre, 1993; Schabenberger and Gotway, 2005). Swihart and Slade (1985) suggested that serial autocorrelation in animal locations affected the size of home range estimates and violated the statistical assumption of independence of observations. When observations are dependent, normal regressions based on stationarity (*i.e.*, uniform variance in the predictor variables) fail (Weisberg, 2005). This often results in the inflation of Type I errors in hypothesis testing (Legendre, 1993), due to the underestimation of sample variance because of spatial autocorrelation. Otis and White (1999) proposed sampling at longer time intervals to reduce spatial autocorrelation in location estimates, however, this does not eliminate spatial dependence. This led De Solla *et al.* (1999) to study the effect of spatial autocorrelation in home range estimates. They concluded that spatial autocorrelation did not affect home range estimates and that it was an acceptable consequence as independence in individual animal locations was not ecologically meaningful. Lichstein *et al.*, (2002) Krausman that spatial autocorrelation affected parameter estimates and coefficients which results

in differences between spatial and non-spatial regression models. Hepinstall *et al.* (2003) well aware of the influence of spatial autocorrelation in measuring resource selection by Stellar's Jays used non-linear spatial autoregressive models found that it did not significantly alter conclusions regarding selection. Non-random space use by individuals in response to heterogeneous vegetation patterns is a characteristic feature of landscape ecology (Pickett and Cadenasso, 1995).

Li and Reynolds (1994) defined spatial heterogeneity as an ecosystem pattern characterised by complexity and variability. This ecological property involves patch shape, patch type, patch size, spatial arrangement, and contrasts between adjacent patches. Spatial heterogeneity influenced habitat selection by elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) by affecting the spatial aggregation of food patches (Anderson *et al.*, 2005; Kie *et al.*, 2002). Kutilek (1979) recognised vegetation heterogeneity as an important feature in home ranges of non-migratory herbivores. Areas had distinct vegetation types that sustained the animals at different periods of the year. Use of GIS and remote sensing technologies has enhanced the use of RUFs by providing for the analysis of resource section at multiple spatial and temporal scales (Boyce, 2006). The scale-dependent nature of habitat selection by herbivores affects sensitivity of RUFs, especially the identification of resource perception scales (Senft *et al.*, 1987). Johnson *et al.* (2002) detected habitat selection by caribou (*Rangifer tarandus caribou*) at large scales (*e.g.*, 2 km) compared to lesser scales. Kie *et al.* (2002) suggested mule deer (*Odocoileus hemionus*) selected habitats at scales larger than the home range. These studies confirm that herbivores respond to vegetation patterns in landscapes at large scales but foraging decisions are made at

smaller scales (Senft *et al.*, 1987). MacArthur and Levins (1964) distinguished between "fine-grained" and "coarse-grained" habitat selection. Animals that perceive landscapes as uniform patches, possibly due to the small and/ or imperceptible grain sizes are described as fine-grained individuals and therefore do not select for habitats, whereas coarse-grained individuals distinguish between habitat attributes and select significant aspects (*e.g.*, avoiding areas with more woody cover as an anti-predator strategy). Resource utilisation functions can be used to identify scales of resource perception by individuals according to this formal classification. Resource utilisation functions have not been fully adapted to large-scale in habitat use studies on African mammals. This may be due to prohibitive costs of telemetry equipment, funding constraints and expertise lack of expertise in this field.

1.5.4 Sable Antelope Ecology and Habitat Use

The sable antelope in southern Africa, *H. n. niger* is one of three subspecies of *H. niger*, the others *H. n. variani* and *H. n. roosevelti* are found in Angola and East Africa respectively (Estes and Estes, 1974; Skinner and Chimumbira, 2005). The southern African variant *H. n. niger* has the largest distribution range (Skinner *et al.*, 2005). Sable antelope are gregarious, medium-sized grazers with an average body mass of 227 kg (Estes, 1997). A herd of about 15-30 individuals composed mostly of females, calves, sub-adults (Estes and Estes, 1974; Estes, 1997). Sable antelope herds are cohesive and are maintained through having a stable social structure (Estes and Estes, 1974; Sekulic, 1981). Males are territorial and defend

their territories from other males. About 20-25 sable antelope roam the Punda Maria section of KNP and approximately 450 animals remain in the entire park.

Sable antelope habitats include the following landscape level vegetation associations: forests (Sekulic, 1981), open woodlands, xerocline slopes, vleis, and grasslands with medium-tall grasses (Ben-Shahar and Skinner, 1988; Magome *et al.*, 2008; Parinni, 2006). Grass species consumed by sable antelope include *Panicum maximum*, *Themeda triandra*, *Eragrostis superba*, *Chrysopogon* spp., and *Andropogon* spp. among others (Grobler 1981; Wilson and Hirst, 1977; Ben-Shahar and Skinner, 1988).Most of these grass species grow in areas with low woody cover where they may have less competition for sunlight, water and nutrients (Medina and Silva, 1990; Pellew, 1983). Shade tolerant grass species like *P. maximum are* frequently eaten by sable antelope, partially due to their high nutritional value and moisture content (Parinni, 2006). Wilson and Hirst (1977) compared woody canopy cover (tree cover) in areas occupied by sable antelope in South Africa and Zimbabwe. They reported that total woody cover ranged between 8.9-24.9%, with tree canopy cover making a significant contribution. However, variability in cover estimates may be due to differences in vegetation communities but because sable antelope habitat use is variable throughout the course of the year, hence it is difficult to generalise. Based on the optimal foraging theory, sable antelope are expected to choose open areas which allow them to maximise food intake because of grass abundance but which may be of low quality due to increased steminess. However, since forage of higher quality is associated with woody cover (Ludwig *et al.*, 2008), and since sable antelope are

food specialists (*e.g.*, selecting high quality grass stems of *P. maximum*); they are expected to straddle between the two cover types (intermediate cover).

However, because sable antelope occur at relatively low population densities, the predation avoidance hypothesis (Hirth, 1977) predicts that they should favour areas with more woody cover relative to surrounding areas. The giant sable antelope in Angola and the Kenyan subspecies do occur in areas with a higher density of woody cover. Sable antelope have distinct wet season and dry season use areas (*i.e.*, home ranges), although they may overlap, (Estes, 1974; Wilson and Hirst, 1977), each with its own woody cover characteristics. Harrington *et al.* (1999) also concluded that habitat selection by rare antelope was more evident in the late dry season where food resource and water were limiting factors. Ogutu and Owen-Smith (2005) suggested that drought mediated moisture loss in habitats adversely affected the nutritional content in sable antelope diets and this reduced fitness levels. Grobler (1981) observed that the body condition of sable antelope deteriorated during the late dry season when food was limiting. During lean periods, sable antelope spent more time feeding in open areas in the Matopos National Park, Zimbabwe (Grobler, 1981). If sable antelope in KNP adopted a similar strategy in response to identical constraints, then their predation risk is likely to have increased, particularly because large predators are more abundant. Owen-Smith and Mills (2006) suggested that predation by lions (*Panthera leo*) was responsible for decline in sable antelope populations, and that lion numbers had increased in response to growing prey abundance in the northern plains. Predation pressure in Matopos National Park is likely to have been less than that at KNP because of the absence of large predators such as lions. The

relationship between total woody cover (shrub and tree cover) and space use has not been investigated using RUFs (*e.g.*, Wilson and Hirst, 1977).

Resource selection by ungulates as outlined above is dependent on habitat attributes and animal behaviour. The accurate assessment and measurement of these variables allows one to quantify habitat selection. Habitat attributes associated with woody cover include soil nutrients, plant availability and distribution, and temporal variation in leaf phenology. The animal behavioural aspects covered were herd size, predation and ungulates response to these and habitat attributes. Because resource selection decisions are spatial, it was established that the most useful models of space use were probabilistic ones that enable amount of use and location to be quantified. The use of GPS collars has resulted in the accurate location data in wildlife studies and this has resulted in the robustness and breadth of habitat use studies. Marzluff *et al.*'s (2004) UDs and RUFs were favoured because they met these two requirements (habitat attributes and animal spatial behaviour) in assessing woody cover selection by sable antelope.

CHAPTER TWO

2. Materials and Methods

2.1 Study Area

Punda Maria is located in the northern plains of KNP in the Limpopo Province of South Africa (Figure 2.1). This area is located in the flat Limpopo-Sabie basin, characterised by a few hills (Eckhardt *et al.*, 2000). Granite rock forms the dominant substrata. The common soil type is the alluvial sands (Eckhardt *et al.*, 2000), while fersalitic clays and smectitic soils are also present. The rivers flowing through this region are mostly ephemeral but may have permanent pools. The rivers include the Mphongolo, Marithenga, and the Gupula among others. Woody vegetation in the area is comprised of a mix of broad-leaf and narrow-leaf woody species interspersed with grasses. *Colophospermum mopane* (both tree and shrub) dominate woody cover, with the former being the most abundant. Other common tree species include *Terminalia sericea, Combretum colinum, C. apiculatum, C. imberbe, Afzelia quanzensis* and *Acacia nigrescens*. The area has a warm-wet season (October-March) and a cool dry season (April-September), and the annual rainfall averages 650 mm per annum (Gertenbach, 1980). The common ungulates in the area include zebras (*Equus burchelli*), kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellisyprimnus*) African buffalo (*Syncerus caffer*) and the blue wildebeest (*Connocahetes taurinus*).

2.2 Overview of Study Design

A Type II study design, whereby locations are collected at the individual but resource availability defined at the population level (Thomas and Taylor, 1990) was used in this study because there was a collared sable antelope and its behaviour was assumed to represent that of the maternal herd. This was a limitation in the study because animals have different movement patterns even when they belong to the same group (Hansteen *et al*., 2002; Johnson *et al*., 2002; Marzluff *et al*., 2004). However, since sable antelope maternal herds can be considered cohesive (Sekulic, 1981), I therefore assumed that the behaviour of the individual collared sable antelope did not differ from that of the herd. However, it was not possible to test for this due to the high cost of GPS collars.

Since sable antelope habitat use changes with season, the years were divided into wet and dry seasons depending rainfall amount and historical rainfall data. Home ranges and UDs were estimated for each season. I used two methods to estimate woody cover 1) dot-grid method, 2) OBIA and validated them with field data. The dot-grid woody cover estimates were used to check the reliability of OBIA cover The most reliable woody cover estimate (*i.e.*, the dot-grid method) was used to develop RUFs that regressed woody cover on UDs from randomly selected seasonal UD pixels using ordinary least squares (OLS) regression. The flow diagram of the research design is given below (Figure 2.2 overleaf).

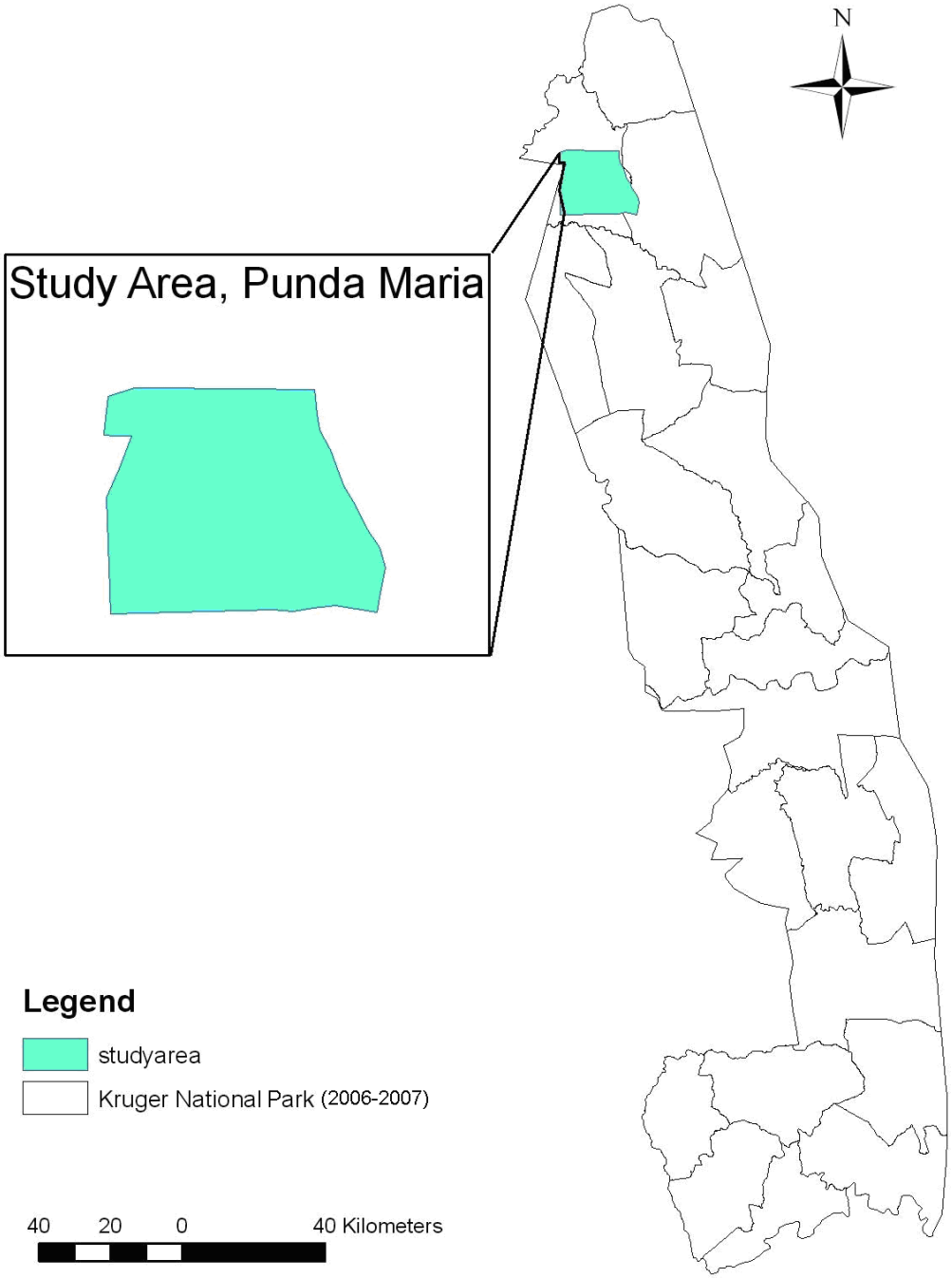


Figure 2.1: Location of study area in the Punda Maria Section of KNP

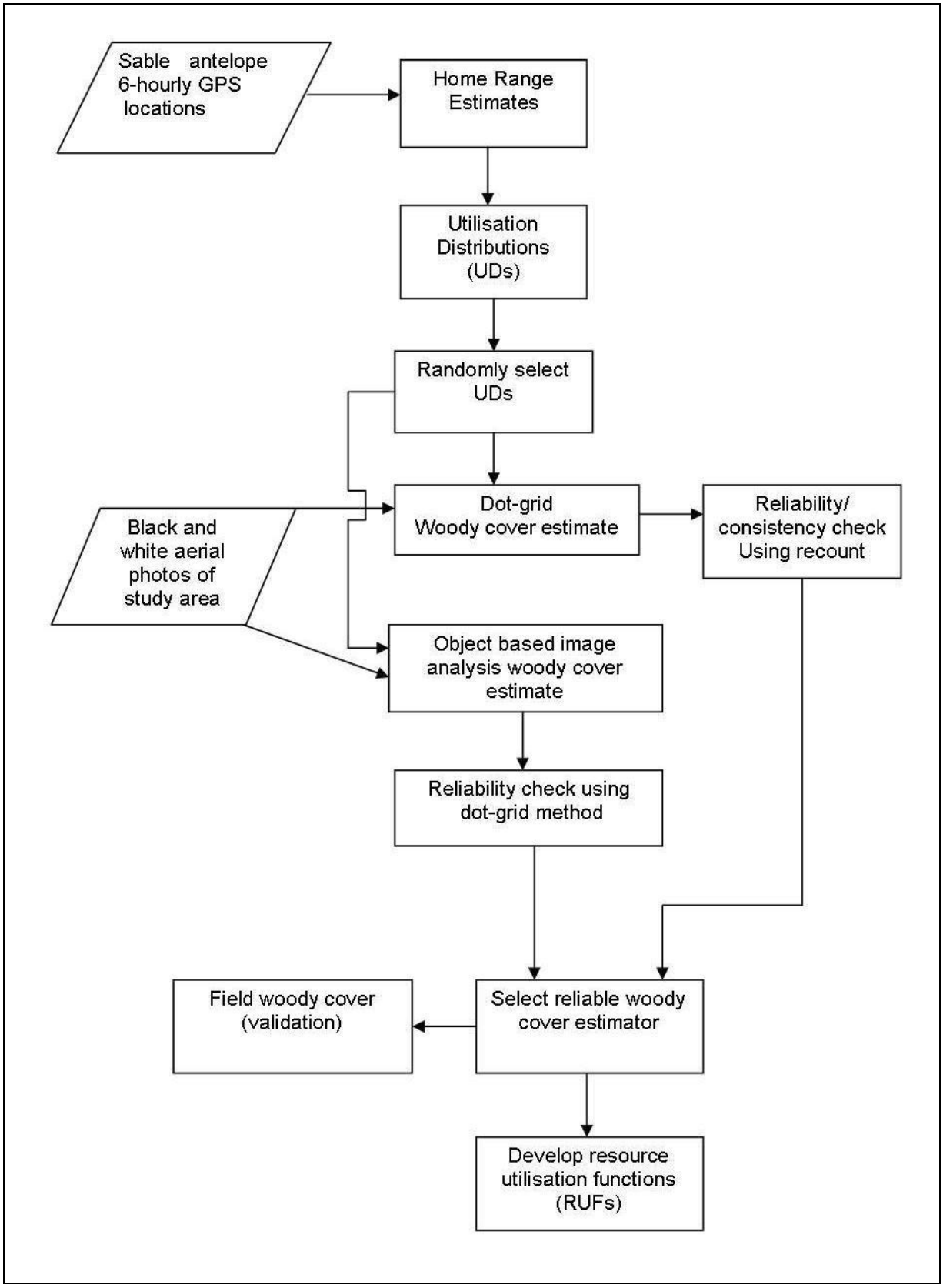


Figure 2.2: Diagrammatic overview of study design

2.3 Seasonal Home Ranges

Rainfall data from the Punda Maria weather station for the period October 2006 to August 2007 were incorporated with Gertenbach's (1980) record to separate the wet and dry season (Figure 2.3). The wet season rainfall started later than usual (October) as rain began falling from November 2006 and ended in April 2007, while the dry season was from May 2007 to August 2007. Global positioning systems telemetry data from collared sable antelope was continuously collected using a 6-hour interval GPS fix via GSM (cellular network). Africa Wildlife Tracking (http://www.awt.co.za) supplied the GPS/GSM collar AM143. Data collection was at six-hour intervals to reduce serial and spatial autocorrelation in location estimates (Hansteen *et al.*, 2002; Otis and White, 1999; Swihart and Slade, 1985). The collection times were at 0200, 0800, 1400, and 2000hrs. No attempt was made at correcting for missing locations, as this was not in the scope of the present study. There were 653 locations collected in the wet season and 404 locations in the dry season. The GPS points that corresponded to some suspected water routes (these also included isolated points) during the dry period, were deleted and these were more numerous in the dry season (Appendix 1a and 1b). This ensured that locations corresponding to the activities of interest such foraging and resting were captured with minimum distortion. The telemetry data were available in the geographical coordinate system (decimal degrees) using the World Geodetic System (WGS) 1984 map datum. The location data were projected to the zone 36S Universal Transverse Mercator (UTM) Projected Coordinate System while maintaining the WGS 1984 map datum, which is correct for the calculation of distances and areas in southern Africa. Separate home ranges

for the wet and dry season were estimated using a 50% and 95% fixed kernel home ranges and smoothed using the LSCV method using Home Range Tool for *ArcGIS* 9.x (Rogers *et al*., 2005). The LSCV smoothing parameter was used for the shape of the kernels as it is recommended for the fixed kernels (Kernohan *et al*., 2001; Seaman *et al.*, 1999). Optimal smoothing of the home ranges was achieved with a raster resolution of 50 m. Utilisation distribution contours within the home range were divided into two probabilities of use contours isolines/ contours [*i.e.*, the 50% core use (KI50), and the 95% non-core use (KI95)].

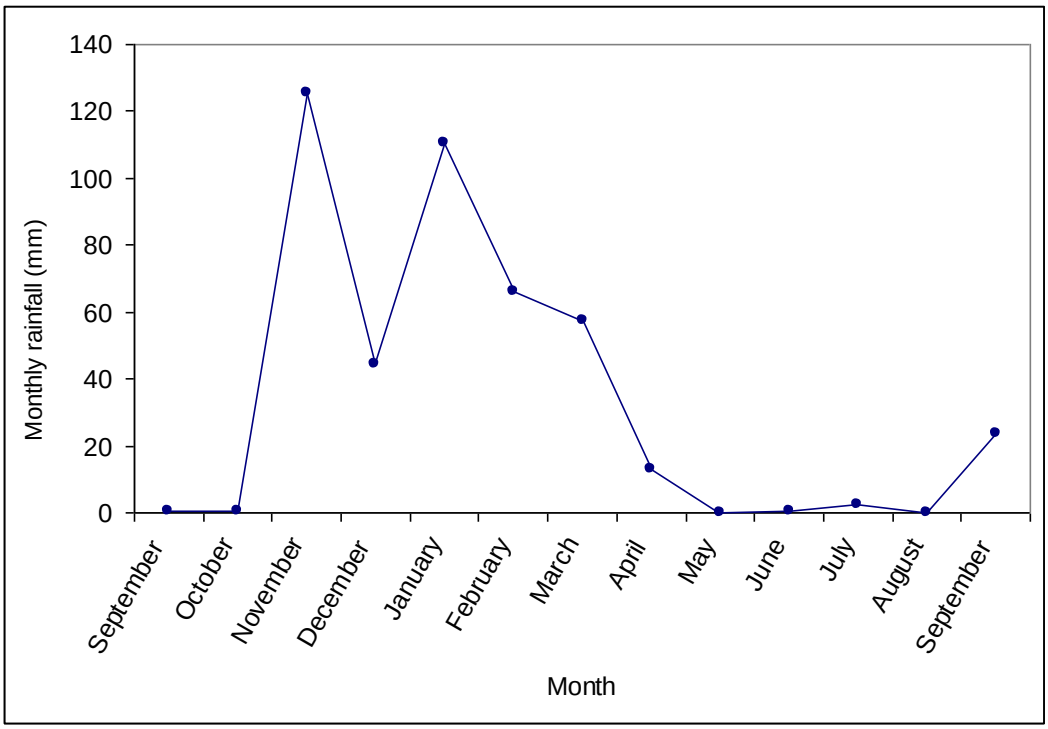


Figure 2.3: Punda Maria rainfall data for the period September 2006 - September 2007
(*Source*: Punda Maria station)

2.4 Utilisation Distributions

The probability of space use within home ranges by animals can be measured with UDs using fixed kernels. The smoothing parameter [*h*] determines the shape of the UD and home range. In this study, fixed kernel density estimates were used instead of standard LSCV smoothed UDs from the projected telemetry data for the two seasons at a raster resolution of 200 m in ArcMap using in Hawth's Tools (Appendix 2a and 2b; Beyer, 2004). Smoothing parameters of 300 were used for the UDs since they approximated the shapes of the seasonal home range contours using least squares cross validation. This limited alternative to the conventional LSCV smoothing parameter was opted for since Hawth's Tool in Arc Map did not have an LSCV option. A scaling factor of one million was selected since kernel density values are usually small. The brightness of the UDs rasters was indicative of the intensity of space use. The UD rasters were clipped to the extent of their respective home ranges.

Kernel density values for the UDs for the polygons were obtained from the UD rasters by running the neighbourhood statistics function in Spatial Analyst (ESRI, 2006). A total of 211 grids in wet season home range and 685 grids in the dry season home range with areas greater than 38 000 m^2 were selected for further analysis because they covered at least 95% of a grid area. This resulted in 211 UD grids for the wet season and 29 in the 50% home range core area (KI50) and 182 in the 95% home range non-core area (KI95). All the UD grid cells for the wet season KI50 were sampled and 60 were randomly sampled in the KI95, making up a sampling frame of 42%. There were 685 dry season UD grid cells. Eighty

grid cells were randomly sampled in the KI50 area and another 112 in the KI95, making up 28% of the sampling frame.

2.5 Measuring Woody Cover

Woody cover in the study was the sum of tree and shrub aerial crown covers. This measure incorporated canopy and shrub cover and associated standard errors in measurements. Total woody cover in the seasonal UD grids was measured from panchromatic aerial photographs using the dot-grid method (Dublin, 1991; Appendix 3), and cropped sections (excluding the dark edges) of images covering the home ranges were subcontracted out for OBIA using Definiens Developer 7 (Definiens Imaging, 2007). Pre-processed orthorectified photos at a scale of 1: 32 000, a spatial resolution of 0.75 m and a root mean square error of 0.04 m were obtained from the Department of Land Affairs South Africa (Surveys and Mapping, 2004). The images were projected to UTM zone 36 WGS 1984-Projected Coordinate System from their original Gauss Conform coordinate system in ArcMap. All images were converted to ERDAS Imagine image format.

2.5.1 Dot-grid Woody Cover Estimation

Woody vegetation in each UD grid cell was estimated using the dot-grid method. Woody cover was visually resolved using the shape, colour, contexture, and contrast of woody vegetation. A regular 10 m dot-grid with cross hairs at each intersection was generated for each 200 m by 200 m UD sampling grid (Appendix

3). The number of cross hairs intercepting woody vegetation cover (*i.e.*, canopy hits) were expressed as a proportion of the total dots within each sampling grid, and subsequently changed to a percentage. Consistency in dot-grid method was measured using Spearman's rank correlation coefficient by systematically resampling 80 grids after a fortnight, to obtain independent estimates (Zar, 1984).

2.5.2 Object-Based Image Analysis Woody Cover Estimation

Overlapping black and white photographs of the dry seasonal home range (*i.e.,* the larger of the two seasonal) home ranges were imported to ERDAS Imagine (Figure 2.4; Leica Geosystems, 2006). A 3x3 low-pass filter was used to remove radiometric noise from the images by averaging neighbouring pixel values (Lillesand and Kiefer, 1994). Filtering ensures that features such as trees and/ or shrubs are represented by fewer polygons (*i.e.*, objects) due to the homogenization of neighbouring pixels (Laliberte *et al.*, 2004). Image segmentation merges pixels into objects used in the final classification. Object characteristics such as colour, size, shape, texture, and brightness are used at different levels of segmentation. A multi-resolution segmentation and classification approach was conducted on the images with minor modifications after Levick (2008) and Laliberte *et al*. (2004) in Definiens Developer 7 (Definiens Imaging, 2008). A fine-level image segmentation approach was used to identify individual shrub and tree canopies and clumps (Figure 2.5) from aerial photograph sections (*e.g.*, Figure 2.5). A level one image segmentation parameters was carried out using the following

parameters: scale (3), colour (0.8), compactness (0.2), shape (0.2) and smoothness (0.8).

There were differences in the brightness levels of images because of burn scars and excessive lense fall-off effect at the edges. These images were done separately with minor modifications to the rule-set. The output polygons from image segmentation were converted to the ERDAS imagine raster format in ArcMap.

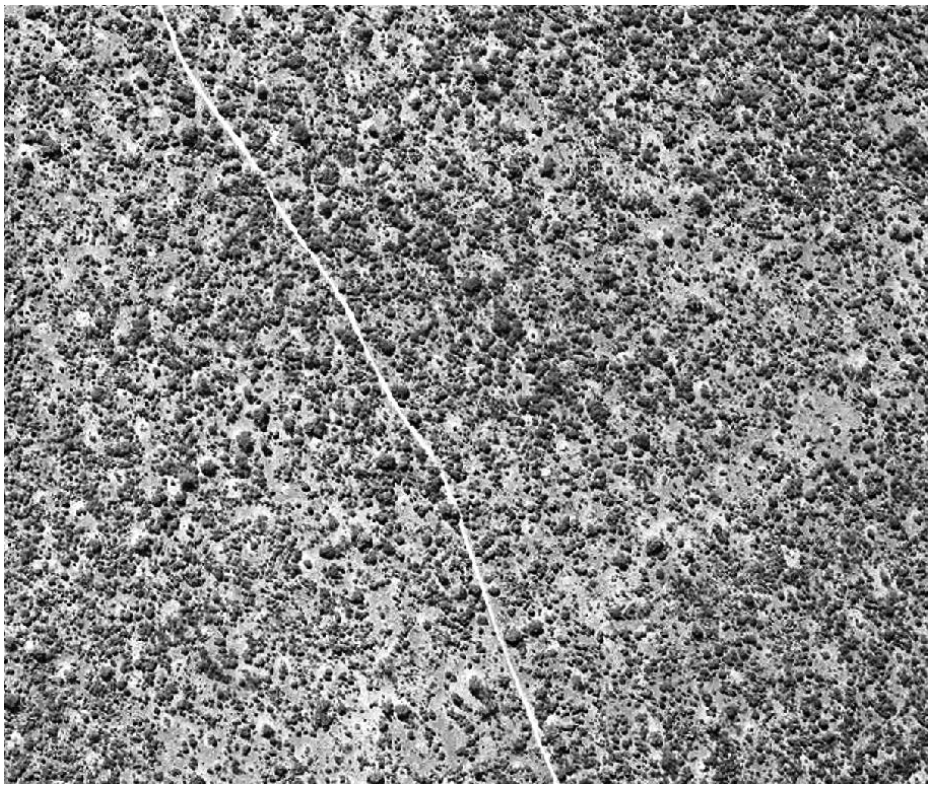


Figure 2.3: Aerial view of woody cover used for dot-grid cover estimates

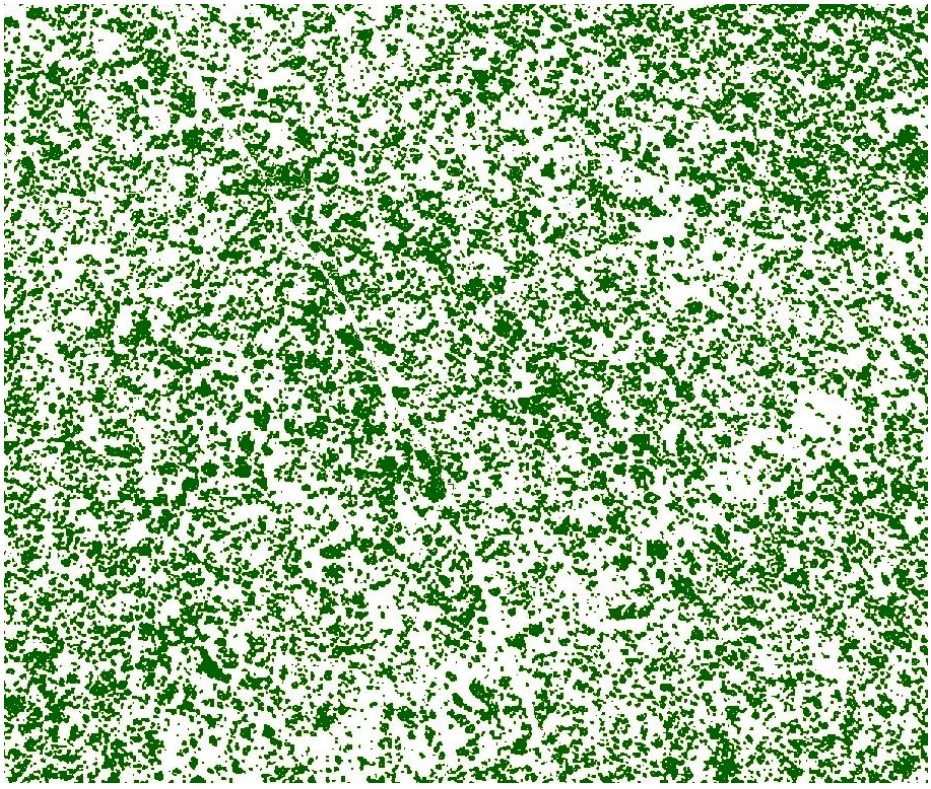


Figure 2.4: Object-based image segmentation of woody cover in Fig 2.4

2.5.4 Comparisons of Woody Cover in Use Areas

Mean woody cover in seasonal UD grids was compared within use areas (*i.e.*, KI50 versus KI95) and between seasons (*i.e.*, dry season KI50 versus wet season KI50) using two-sample t-tests assuming unequal variances (Zar, 1984). All means were presented with associated standard errors. Although two sample t-tests require independent among observations (Zar, 1984), I used them for comparison well aware of possible Type I errors due to the overestimation of pooled sample variance. I assumed that locations were independent of the collared animal for convenience. For the within-use area comparisons, mean woody cover in KI50 was compared to the KI95 area in each seasonal home range. The

between comparisons compared corresponding use areas in the seasonal home ranges. The measures of the means and standard errors were reported.

2.5.5 Comparison of Woody Cover Metrics

A small-scale (1ha) study was conducted to relate tree canopy cover to aerial woody cover. Thirty randomly selected 1 ha plots in the KI50, KI95, and unused/ available areas in the study area were used. Tree canopy cover in the field was obtained with the use of a spherical densiometer (model C) using Strickler's modification (Strickler, 1959). Twenty-five points were sampled in the 1ha plots in a 20 m x 20 m lattice, with the distance between the 16 outermost sampling points and the edge of 10 m all-round (Appendix 4). Aerial woody cover was collected using a 1ha dot grid with 10m cross hair intervals. The two measures of percentage woody cover were correlated to determine if there were relationships using the Spearman's correlation coefficient (Zar, 1984).

2.6 Developing Resource Utilisation Functions

Woody cover at each sampling grid was related to corresponding kernel density value in UD. Linear and non-linear models were used to test for relationships. Linear relationships were investigated using OLS regression:

$$y_i = \alpha + \beta x_i + \varepsilon \qquad (2.1)$$

where y_i is the response variable (kernel density) for each value of the predictor variable x_i (woody cover). The estimated parameters for the models were α (*i.e.*, the y intercept at $x = 0$), β (the slope defined as the unit change in x,

with a unit change in *y*), and ε is the error term that assumes they are normally distributed (Zar, 1984). The predictor variable (woody cover) was $\log_{10}$ transformed to correct for errors and achieve a linear mean function (Weisberg, 2005).

2.7 Software Packages

Software used in analyses were *ArcMAP® 9.2*, *ERDAS Imagine 9.1*, *Hawth's Tools®*, *Spatial Analyst®*, *Home Range Tool® for ArcGIS 9.x*, *Spatial Analysis in Macroecology* and *R Foundation for Statistical Computing* (R Development Core Team, 2008).

CHAPTER THREE

3. Results

3.1 Home Ranges

Sable antelope wet season 95% home range kernel was estimated at 14.1 km^2 and 2.8 km^2 in KI50 isolines (Figure 3.1). Space use was concentrated on the sand-veld areas characterised by mixed combretum, knob-thorn/ mopane woodland and the mopane woodland ecotone. The dry season 95% home range kernel was estimated at 36.9 km^2 and 7.5 km^2 in KI50 isolines (Figure 3.2). The used area was predominantly in the sand-veld area characterised by knob-thorn/mopane woodland and mixed combretum and *Terminalia* woodlands. The overlap area between the two seasonal 95% home range kernels was 12.5 km^2, representing 88% and 34% for the wet and dry season home ranges respectively.

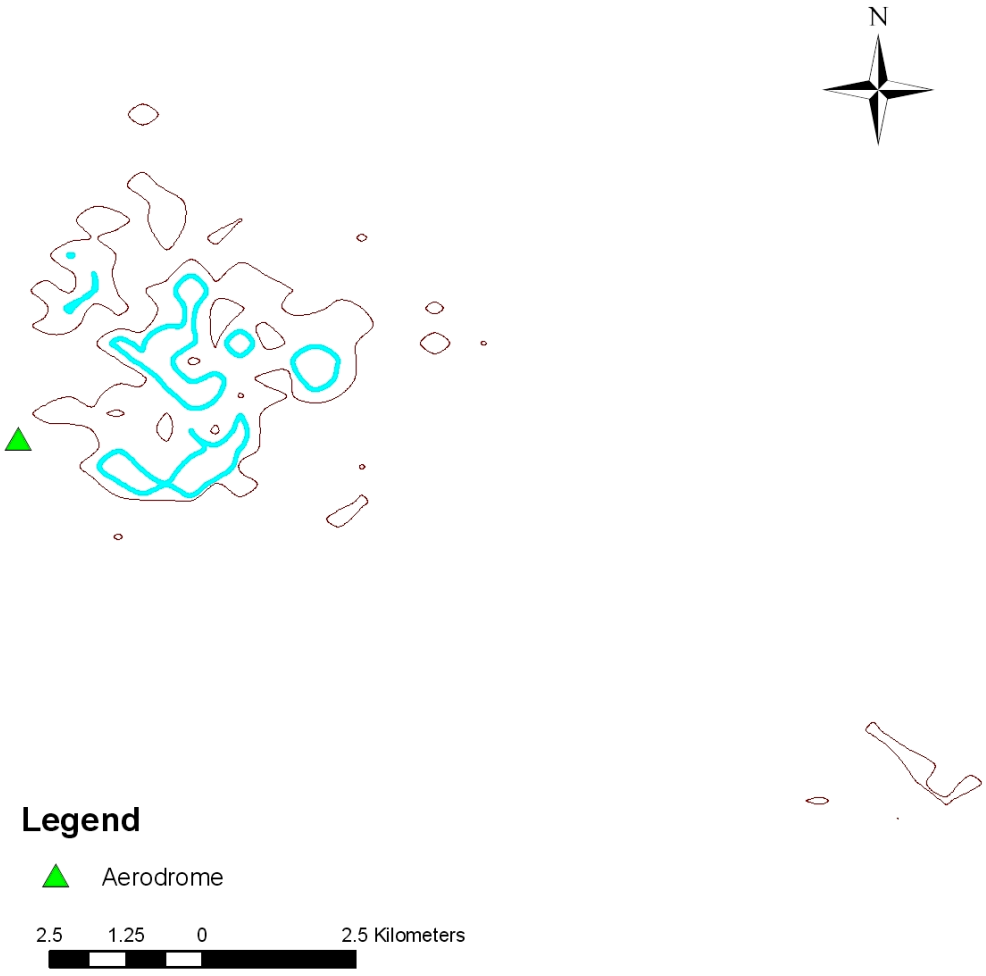


Figure 3.1: Punda Maria Sable antelope wet season (October 2006 – April 2007) home range isolines (The 50% home range isolines are in blue and the 95% home range isolines in brown).

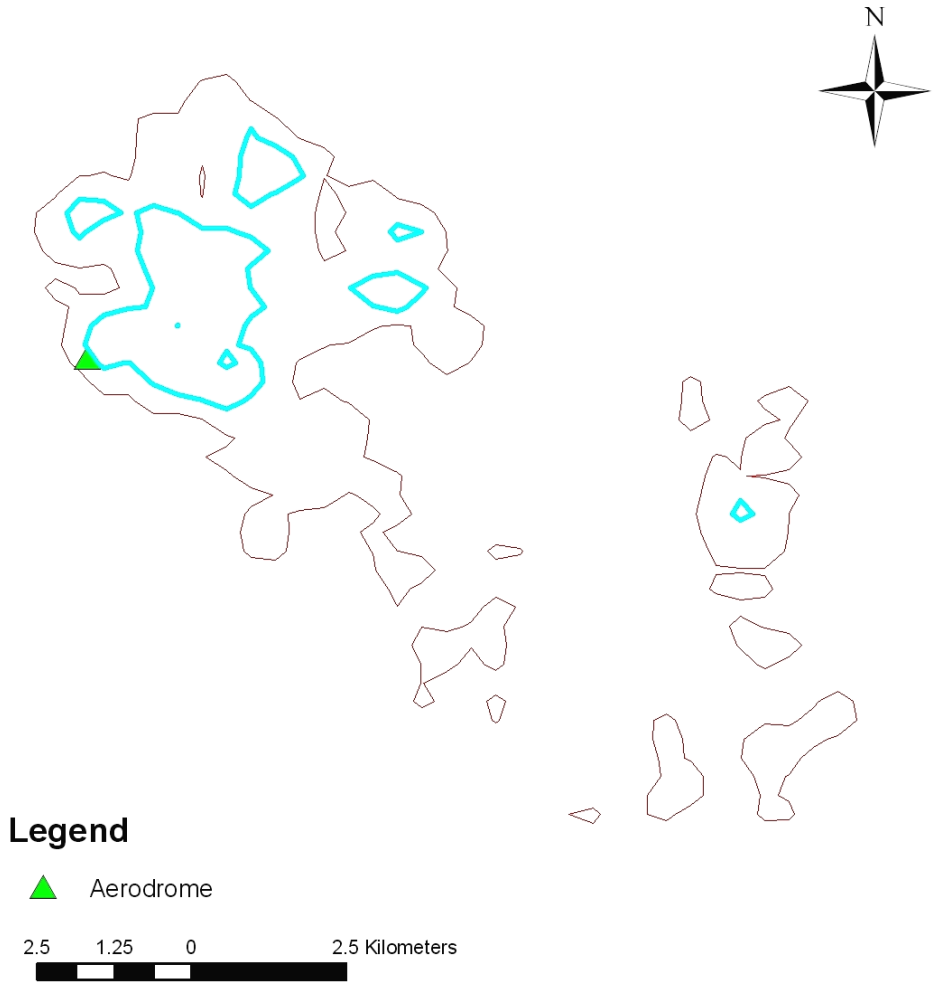


Figure 3.2: Punda Maria sable antelope dry season (May 2007 - August 2008) home range isolines. (The 50% home range isolines in blue and the, 95% home range isolines in brown).

3.2 Woody Cover Validation Estimates

There was significant correlation in the measurement of woody cover from two independent dot-grid estimates of randomly selected UDs between dot-grid measures of woody cover (Spearman's $r = 0.873$, $t_{0.05,\ 78} = 15.823$, $P < 0.001$). Correlation between the dot-grid woody cover and OBI cover was investigated using matching dry season UD grids. Correlation was initially low (Spearman's *r*

= -0.091, n = 66, P = 0.462). The low and negative values may have arisen from poor image quality. The best image (498.455.11.111) with less lense fall-off and burn scars was used. There was a positive correlation between OBI and dot-grid wood cover estimates (Spearman's r = 0.301, $t_{0.05,\ 69}$ = 2.625, P = 0.011), suggesting that image quality played a significant factor (Figure 3.3). Field tree canopy cover from the 30 field plots was positively correlated to dot-grid woody cover (Spearman's r = 0.577, $t_{0.05,\ 1}$ = 3.736, P <0.001).

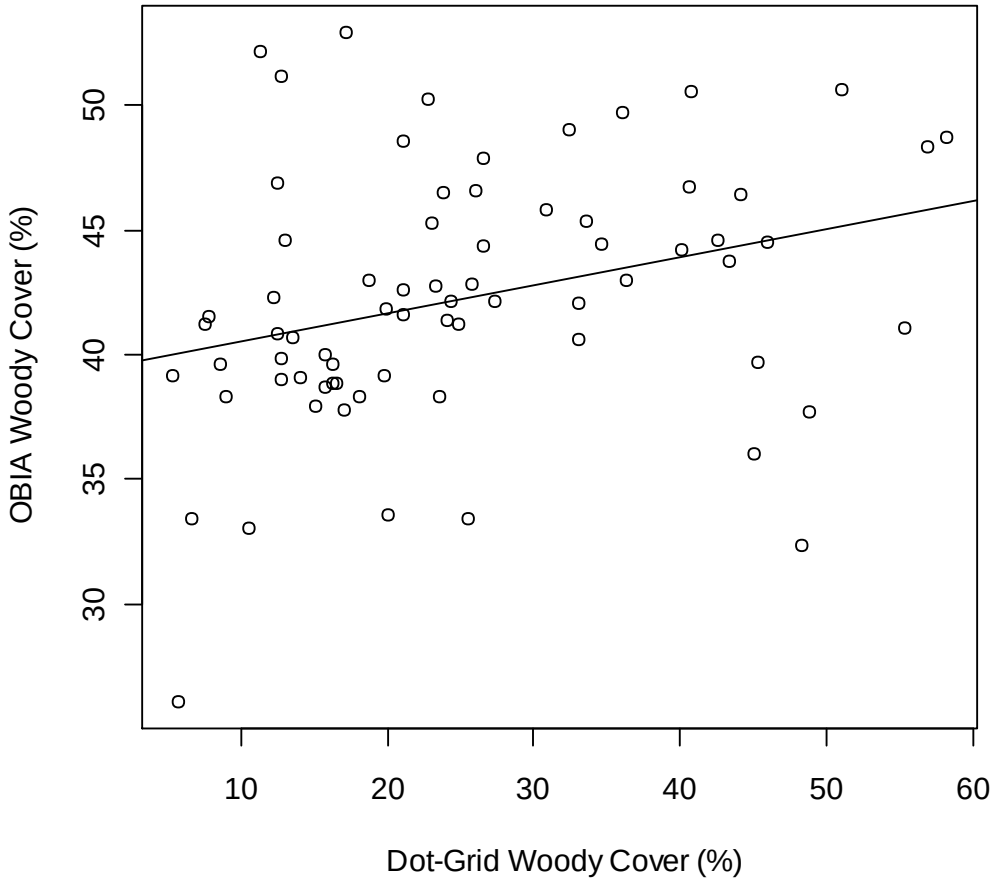


Figure 3.3: Relationship between dot-grid woody cover and OBI woody cover in flight image 498.455.11.111

3.3 Mean Woody Cover Comparisons in Home Ranges

Mean woody cover in the wet season (36.1 ± 1.4%) home range was greater than in the dry season (28 ± 1%) home range ($t_{0.05, 163} = 3.755$, $P < 0.001$).

3.2.1 Dry Season Home Range

Woody cover in KI50 and KI95 areas was 28 ± 1% ($n = 80$) and 31 ± 1.3%) ($n = 111$) respectively. There was significantly more woody cover in KI95 areas ($t_{0.05, 182} = -1.7$, $P = 0.041$) than in KI50 areas.

3.2.2 Wet Season Home Range

The mean woody cover the wet season was 33 ± 3% in the KI50 and 38 ± 2% in KI95. The KI95 woody cover was not significantly greater than woody cover in KI50 areas (, $t_{0.05, 41} = -1.450$, $P = 0.077$).

3.2.3 Comparisons Between Use Areas

Woody cover (33 ± 3%) in the wet season KI50 areas was not significantly greater than that the dry season woody cover (30 ± 1%) in KI50 ($t_{0.05, 38} = 1.444$, $P = 0.078$). However, woody cover (38 ± 2%) in the wet season KI95 isoline was significant greater than in the dry season KI95 isoline woody cover (31.0 ± 1.3%) ($t_{0.05, 137} = 3.447$, $P < 0.001$).

3.2.4. OBIA Woody Cover Comparisons

Dry season RUF OBIA factional woody covers were 40 ± 1% and 38 ± 1% in KI50 and KI95 areas respectively. Mean woody cover was not significantly greater in the KI50 compared to the KI95 areas ($t_{0.05,\ 66}$ = 0.942, P = 0.174). However, there were no differences in fractional mean woody cover in the wet season home ranges between the KI50 and KI95 areas ($t_{0.05,\ 22}$ = -1.098, P = 0.284), with means 37 ± 1% and 40.0 ± 0.4% respectively.

3.4 Resource Utilisation Functions

3.4.1 Dry Season RUFs

There was no significant relationship between sable antelope habitat use and woody cover abundance in the dry season home range (β = -0.003, *S.E.* = 0.004, $t_{0.05,\ 1}$= -0.699, P = 0.485; Figure 3.4). There were also no significant relationships between the dry season KI50 (β = 0.005, *S.E.* = 0.005, $t_{0.05,\ 1}$ = 0.983, P = 0.329; Figure 3.5) and KI95 (β < 0.001, *S.E.* = 0.002, $t_{0.05,\ 1}$ = -0.368, P = 0.713; Figure 3.6).

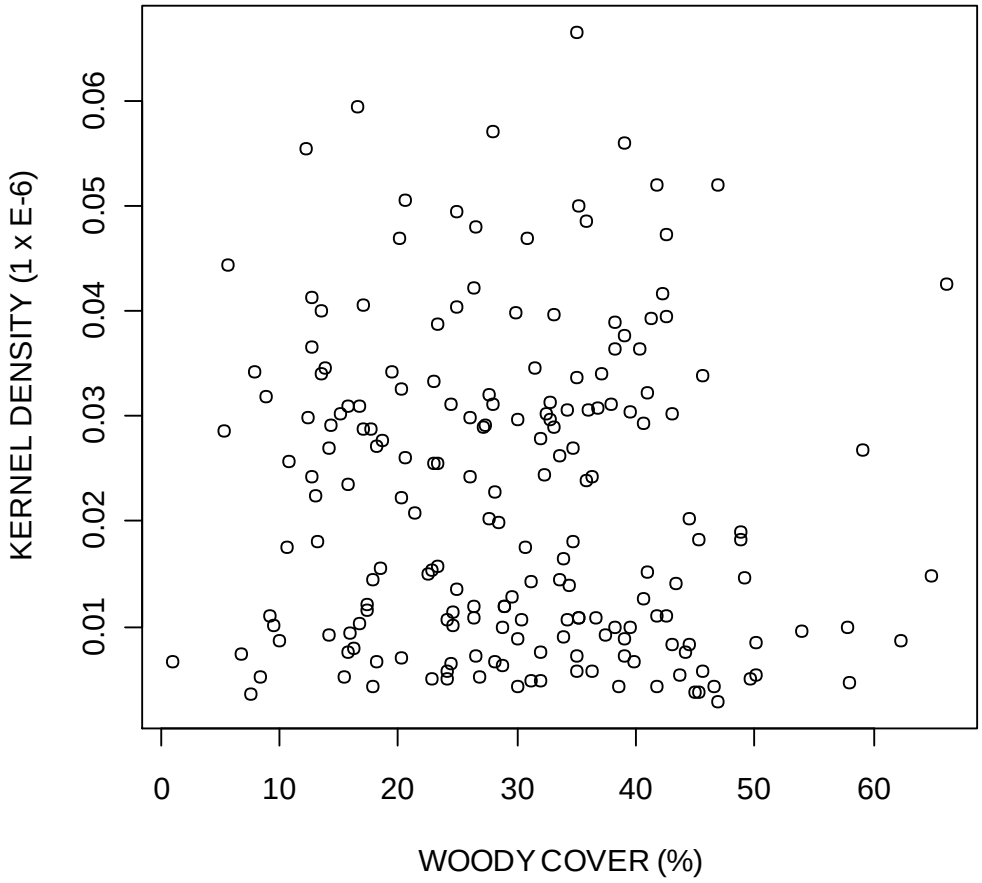


Figure 3.4: Sable antelope dry season (2007) woody cover versus kernel density scatter plot, Punda Maria

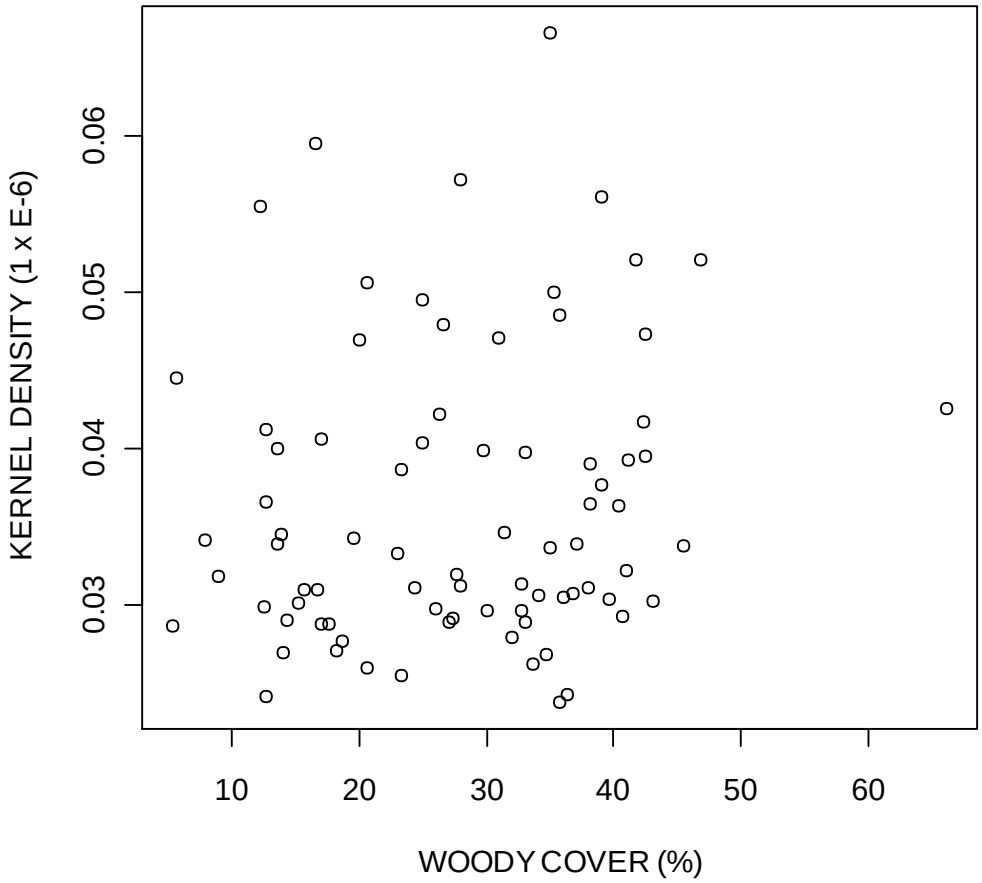


Figure 3.5: Sable antelope dry season (2007) KI50 isoline woody cover versus kernel density scatter plot, Punda Maria

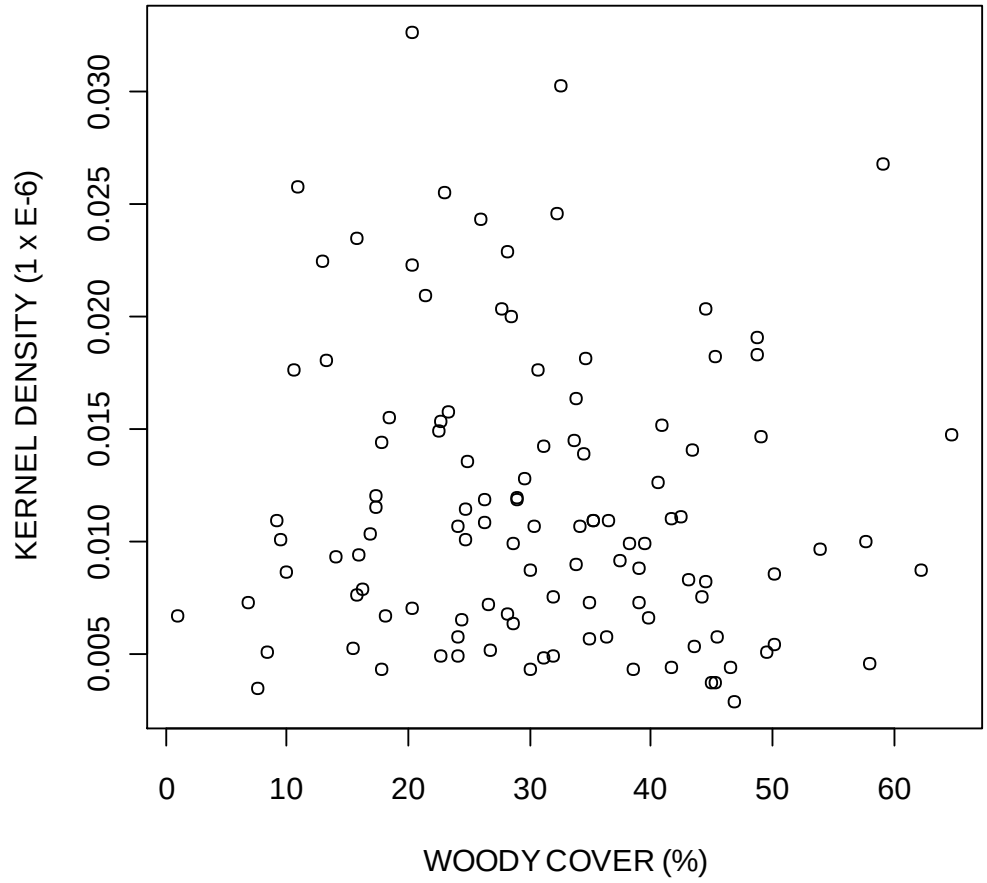


Figure 3.6: Sable antelope dry season (2007) KI95 isoline woody cover versus kernel density scatter plot, Punda Maria

3.4.2 Wet season RUFs

No significant relationships between sable antelope habitat and woody cover abundance were found in the wet season home range (β = -0.014, *S.E.* = 0.009*;* $t_{0.05,\ 1}$ = -1.592, *P* = 0.115; Figure 3.7). I further found no significant relationship between habitat use by sable antelope and woody cover abundance in the KI50 (β = -0.002, *S.E.* = 0.009, $t_{0.05,\ 1}$ = -0.272, *P* = 0.787; Figure 3.8) and KI95 (β = -0.004, *S.E.* = 0.009, $t_{0.05,\ 1}$ = 0.498*; P* = 0.620; Figure 3.9).

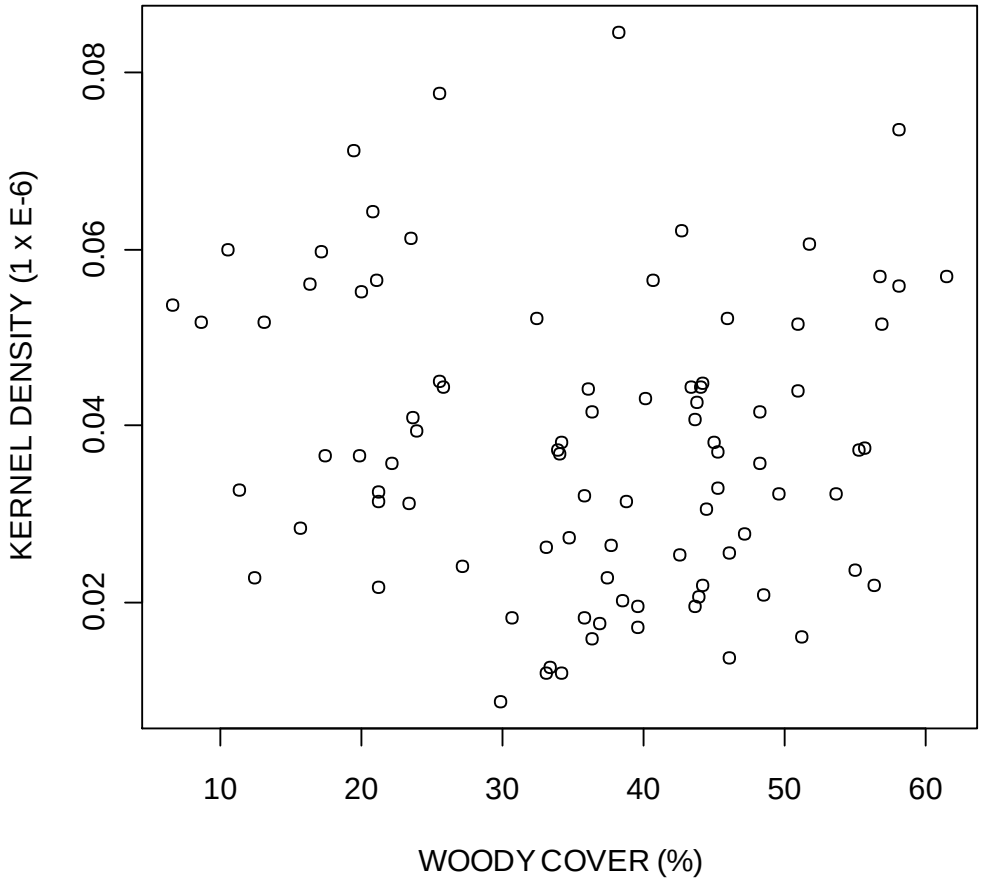


Figure 3.7: Sable antelope wet season (2006-7) woody cover versus kernel density scatter plot, Punda Maria

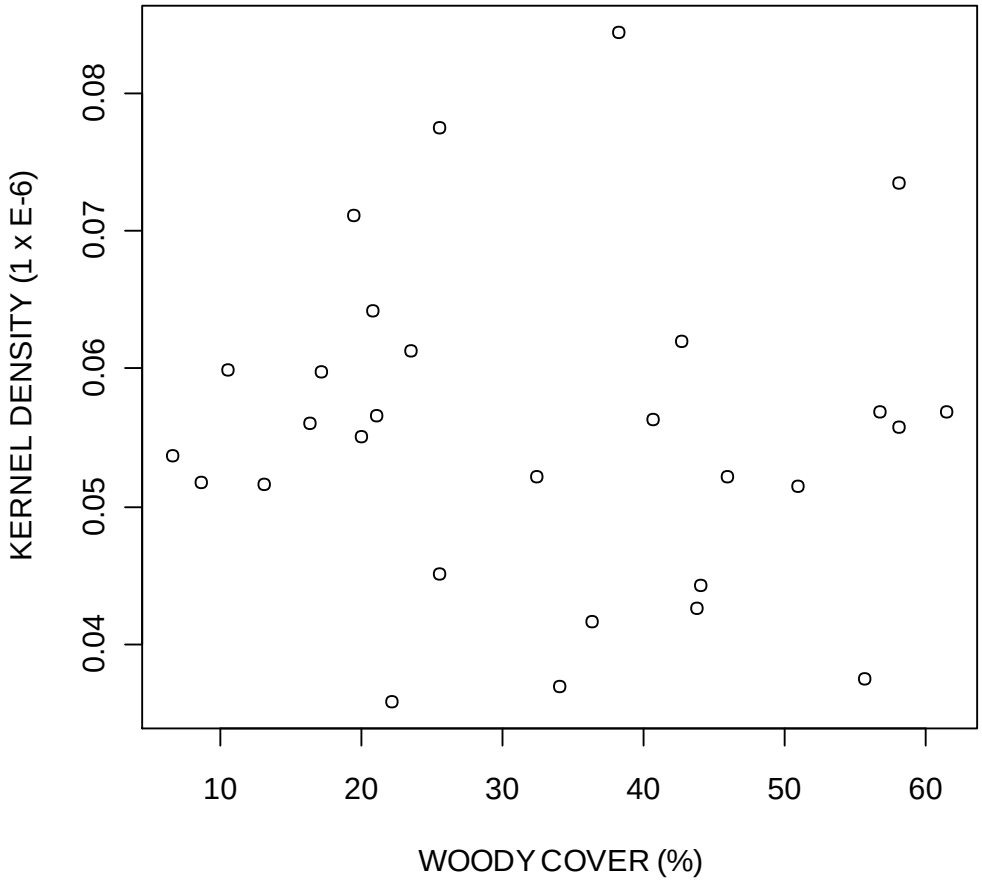


Figure 3.8: Sable antelope wet season (2006-7) KI50 isoline woody cover versus kernel density scatter plot, Punda Maria

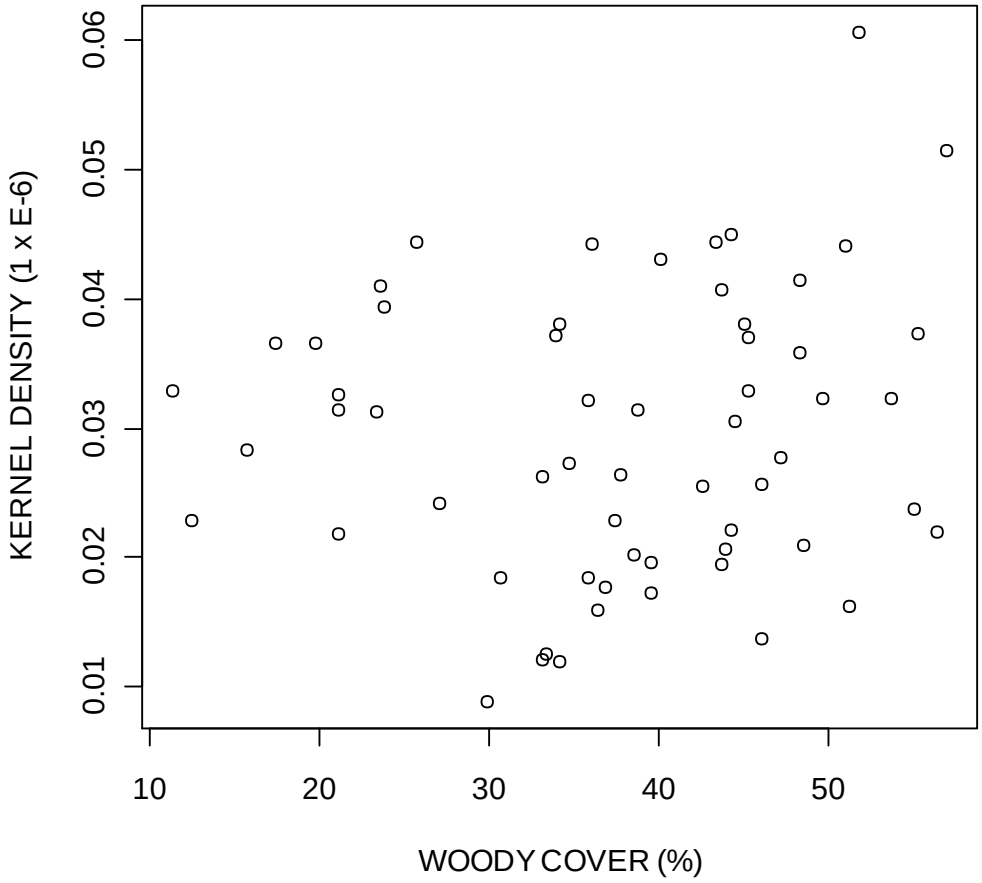


Figure 3.9: Sable antelope wet season (2006-7) KI95 woody cover versus kernel density scatter plot, Punda Maria

3.4.3 Object-Based Image Analysis (OBIA) woody cover comparison

RUFs

I found no significant relationships between woody cover abundance and habitat use by sable in both the dry (β = -0.033, *S.E.* = 0.029, $t_{0.05,\ 1}$ = 1.164, *P* = 0.249; Figure 3.10) and wet season (β = 0.006, *S.E.* = 0.029, $t_{0.05,\ 1}$ = 0.218, *P* = 0.828; Figure 3.11) using object-based image analysis woody cover.

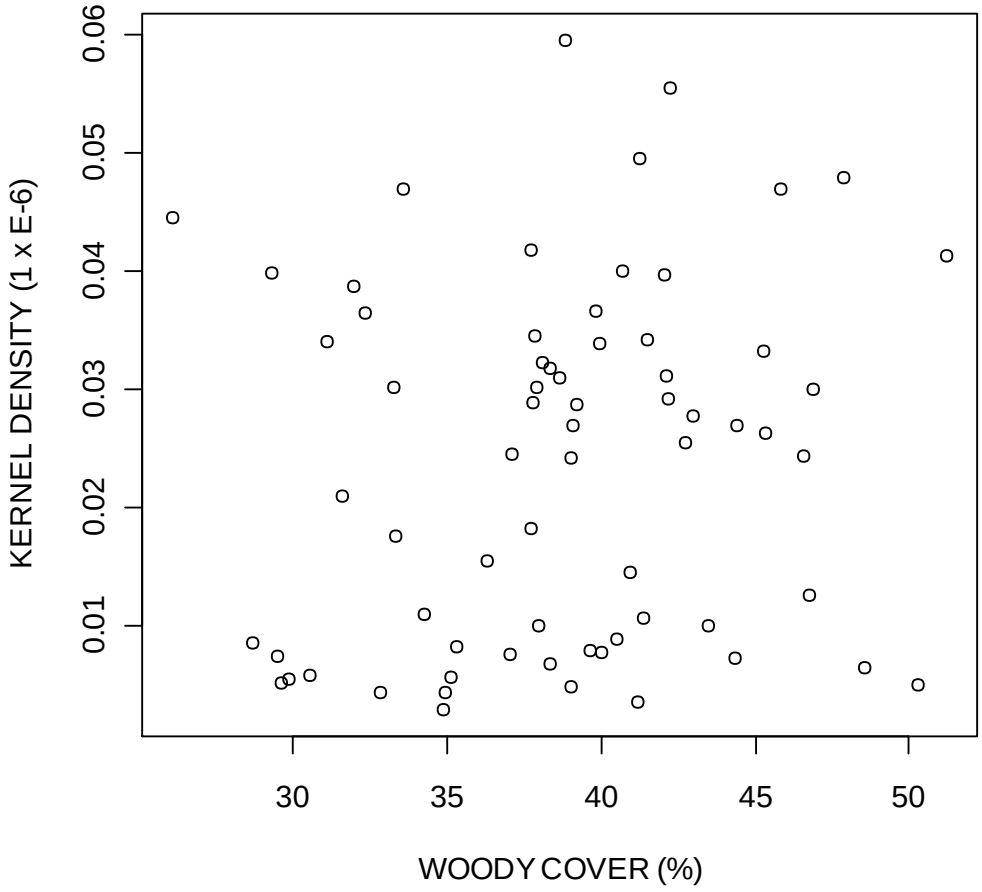


Figure 3.10: Sable antelope dry season (2007) OBIA woody cover versus kernel density scatter plot, Punda Maria

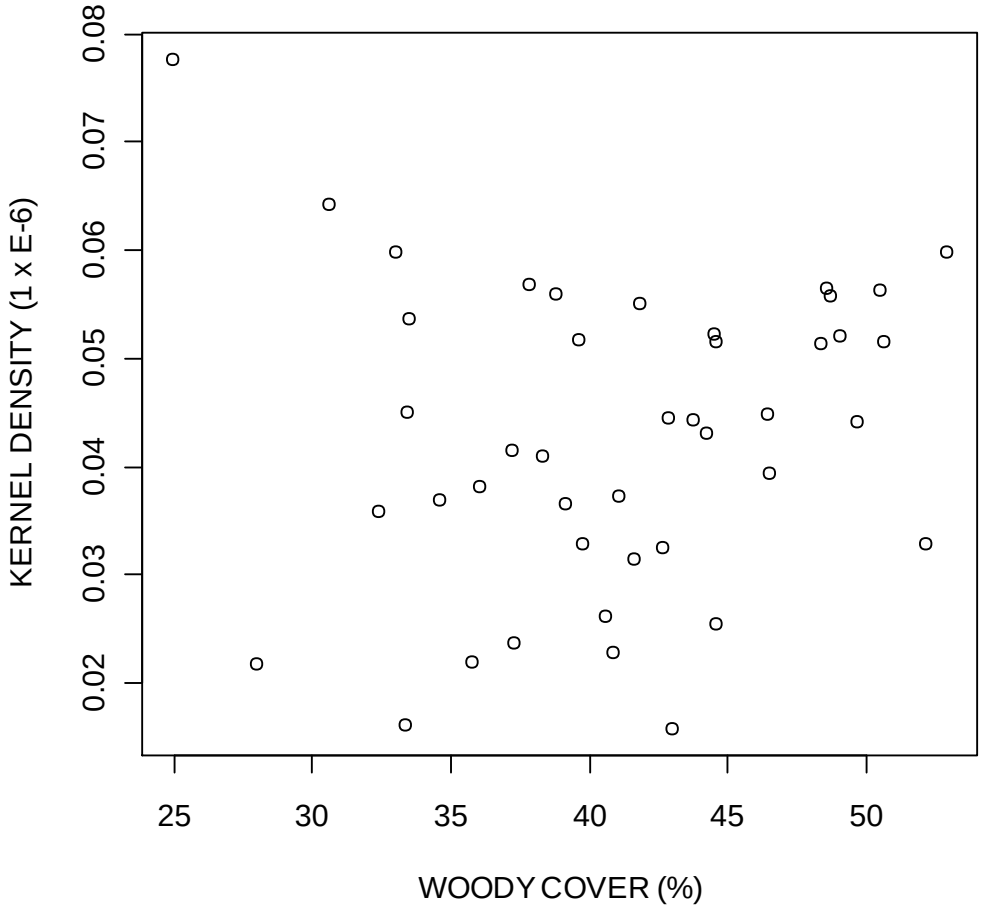


Figure 3.11: Sable antelope wet season (2006-7) OBIA woody cover versus kernel density scatter plot, Punda Maria

CHAPTER FOUR

4.1 General Discussion

There were no significant relationships between habitat use by sable antelope and woody cover abundance at the 200m spatial scale. All the RUF coefficients returned low values further suggesting weak relationships. Results at the scale used in this study suggest that there was no evidence that habitat use by sable antelope was related to variation in woody cover abundance. The predation avoidance hypothesis and foraging maximisation hypotheses were not supported by the results although the general patterns were only indicative. The overall results, though not significant, suggested that habitat use by sable antelope declined with increasing woody cover abundance. Ben-Shahar and Skinner (1987) actually found that sable antelope avoided woodlands with much cover. I expected sable to use area with woody cover because as a predator avoidance strategy and also as a means of maximising the consumption of high nutrient grass.

Jarman (1974) suggested that there are linear relationships between antelope social group sizes and woody cover abundance. Hirth (1977) observed that elk group sizes were smaller in forests when compared with open areas (grasslands). Predator avoidance was proposed to explain similar observations. Woody cover provides concealment cover such that groups with few individuals evade detection by predators in abundant woody cover, while the opposite is true in open areas but compensated for with increased prey vigilance [*i.e.*, more eyes and ears] (Estes, 1974; Hirth, 1977; Riginos and Grace, 2008). There was no way of measuring this phenomenon although this was inferred from the comparing mean woody cover in

the wet season RUF with the dry season RUFs. Mean woody cover in the dry season core areas was less than that in the non-core areas, suggesting that sable antelope avoided areas with more woody cover.

The lack of significant linear relationships between habitat use and woody cover abundance might have been confounded by the fact that home ranges are used for many purposes other than foraging and predator avoidance (*e.g.*, mating, minimization of intra-specific and inter-specific competition, and resting) among other uses. The pooling of the 6-hourly GPS location data may have concealed use patterns (*e.g.*, the 8:00am and 8:00pm locations may have coincided with foraging periods whilst the others may have corresponded to other behaviour). Grobler (1981) noted that sable antelope foraged between 0600 and 0900 and between 1600 and 1700. However, the interval of 6 hours was too long an interval to identify areas used for foraging by large ungulates, and considering that sable antelope move large distances. Franke *et al.* (2004) suggested the use of hourly location data for this purpose. In another case, I would also expect sable antelope to rest in secure areas (*i.e.*, with either low shrub cover and/ or tree cover); hourly locations may also assist in discovering the woody cover attributes in those areas. Attaching ecological value to location data is a major step in uncovering habitat use behaviour.

For example, Newman *et al.* (1995) established that a low increase in predation risk significantly disrupted linear responses to food abundance. The KNP has seasonal rainfall and therefore soil moisture, which affects the growth, nutritional quality, and palatability of grass. However, they decline in the course of the dry season, becoming severe in the late dry season (Ogutu and Owen-

Smith, 2005). Sable antelope frequently moved to sources of water such as the permanent and temporary pools along the Mphongolo River, during the course of the dry season. Not all GPS locations corresponding to water routes were removed because of the lack of data regarding the location of most water bodies that sable antelope use, particularly during the wet season and early dry season when water is available in numerous temporary pans.

Johnson (1980) criticised studies designed for measuring resource selection by animals within habitats (*i.e.*, home ranges). He argued that home ranges represented a prior level of selection of landscape attributes critical to species survival and therefore further investigation of selection within them (*e.g.*, using RUFs) was circular. Large ungulates perceive habitat patches at a large scale (Senft *et al.*, 1987). Kie *et al.* (2003) reported that mule deer selected for landscape features at large scales (*e.g.*, 2 km) compared with smaller scales when using spatially explicit data. Presently, few animal ecologists have incorporated non-stationary spatial statistical analyses in habitat selection studies as these types of analyses may be beyond what they were trained for (Kissling and Carl, 2008; Rangel *et al.*, 2006). Utilisation distributions and woody cover patterns are prone to spatial patterning (*e.g.*, clustering), which is a departure from randomness assumed in parametric statistical tests (Legendre, 1993; Lichstein *et al.*, 2002; Moran, 1950; Schabenberger and Gotway, 2005). The pooling of monthly animal locations to to develop seasonal home ranges may have contributed to high spatial autocorrelation values within home ranges and subsequently the UDs.

Sable antelope home ranges are variable in Africa. Grobler (1974) estimated a home range of 2.6 km^2 in riverine woodlands of the Victoria Falls (Zimbabwe),

while in the Shimba Hills National Park (*i.e.*, a mixed forest and grassland community), home ranges ranged between 10 km^2 and 24 km^2 (Sekulic, 1981). Magome (1991) estimated large home ranges, between 13 km^2 and 44 km^2 in the Pilanesburg Game Reserve (PGR), possibly due to large herd sizes. Rahimi and Owen-Smith (2007) recorded the largest home ranges in KNP ranging between 55 km^2 and 118 km^2. Home ranges in Punda Maria ranged between 14.1 km^2 and 36.9 km^2 for the wet and dry season, comparing well with those in similar geographic regions (*e.g.,* Magome *et al.,* 2008). Although comparable, the home ranges were obtained using different methods. There are different methods available for estimating home ranges (*e.g.*, Getz *et al.*, 2007; Moorcroft *el al.*, 1999). The kernel density method for home range estimation was used in this study because it is accurate, well understood and allows for the creation of UDs (Kernohan *et al.,* 1999; Hepinstall *et al.*, 2003; Seaman *et al.,* 1999). Resource utilisation functions are useful tools for investigating the link between probabilistic measures of space use with landscape-habitat attributes. However, the choice of smoothing parameter [*h*] affects outputs from kernel density estimators and conclusions drawn from them (Silverman, 1986; Worton, 1989). Resultant UDs and RUFs depend on the correct choice of bandwidth as under-smoothing leads to noise, while over-smoothing obscures detail and increases spatial autocorrelation. There is a possibility that UDs in this study may have been under-smoothed, introducing noise.

There was a large difference in size between the wet season (14.1 km^2) and dry season (36.9 km^2) home ranges. The difference could be indicative of the periods of localised food scarcity, compensated for by wide ranging behaviour in

response to patchily distributed resources. Woody cover in the dry season home range was less than that in the wet season indicating that the extension of home range was toward areas of low woody cover. Gureja and Owen-Smith (2002) and Parinni (2006) established that sable antelope used previously burnt areas during the dry season, and these are usually in open areas, which burn more frequently (Sankaran *et al.*, 2004). The extension of home range sizes in the dry season is likely to include marginal foraging sites and optimal foraging sites with increased predation risk. Another plausible explanation could be the presence of distinct habitat use areas (Estes and Estes, 1974). Magome *et al.* (2008) showed that *C. serrulatus* and *P. maximum* significantly contributed to the diet of sable antelope in PGR, while other grass species made variable contributions throughout the year. This observation may explain the overlap between the wet and dry season home ranges due to the patchy distribution of foraging resources (preferred grass species). Wilson and Hirst (1977) found that sable antelope monthly home ranges were variable and were significantly larger during the dry season. Habitat selection by animals occurs at different spatio-temporal scales (Bailey *et al.*, 1996; Senft *et al.*, 1987) yet current home range estimation practises do not discriminate among these contrasting choices. Often the single estimates need objective evaluation. Habitat use decisions by organisms are scale and activity dependent (Wiens, 1989), and therefore habitat selection studies that do not incorporate this aspect in home range estimation can be misleading.

Results from mean woody cover comparisons between the two seasonal home ranges supported the hypothesis that woody cover was more abundant in the wet season compared with the dry season use areas. Sable antelope prefer to

forage in areas with green grass (Parinni, 2006), and when this becomes scarce during the late dry season, they may be forced to move into open areas where other grasses are still abundant. Sable antelope in Punda Maria preferred *P. maximum* to other grass species in the early dry season, but in the late dry season, they were generally foraging on a mix of grass species, most of them growing in open areas (Valerio Macandza, personal communication). My results compare well with those by DelPerno *et al.* (2003) who noted that white-tailed deer maternal herds used areas with more protective cover during summer periods when they reared offspring and open areas during winter when food was scarce. Winter in the northern hemisphere and the dry season in African savannas are similar in that food resources become scarce and of low quality. Grobler (1981) observed that sable antelope frequently used open areas during the dry season and had longer foraging spells. This may have been due to the feeding on moribund grass with low moisture and nutrient quality. This may also explain why sable antelope in this study made regular forays to water points during this critical period. However, increased foraging significantly increases predation risk as it increases the probability of encounter between predator and prey species (Houston *et al.*, 1993; Lima, 1998; Newman *et al.*, 1995). Mangel and Clark (1986) established that domestic sheep subjected to periods of fasting were less vigilant and therefore concentrated on optimising forage intake. Incidentally, Owen-Smith and Mills (2006) suggested that predation on sable antelope by lions (*Panthera leo*) may have caused a decline of these ungulates in KNP, and this could have been more pronounced during the dry season. However, there is lack of compelling evidence to suggest that predators exhibited top-down effects on sable

antelope populations as rainfall amount and timing negatively affected grazing pastures leading to the decline of other ungulates as well (Owen-Smith *et al.*, 2005).

The measurement of woody cover from black and white aerial photographs can present problems (Carmel and Kadmon, 1998; Lu and Weng, 2007). The amount of spectral information is restricted to a single band and this makes the distinction between some features difficult, thereby limiting the performance of traditional pixel-based classification algorithms (Lu and Weng, 2007). Object-based image analysis offers better results because it incorporates pictorial elements such as texture, size and shape (Laliberte *et al.*, 2004; Lu and Weng, 2007), and performs even better when it incorporates ancillary GIS data such as high-resolution digital terrain models. Dublin (1991) noted that the dot-grid method could give variable estimates. The poor correlation between dot-grid woody cover and OBIA woody cover was surprising. This may have been a result of multiple factors including among them poor radiometric resolution of the photographs, spatial heterogeneity and individual bias (Lu and Weng, 2007). The two woody cover estimators had contrasting estimates with the dot-grid method giving conservative estimates in most instances. However, where the dot-grid method gave higher woody cover values, OBIA provided lower values. Tree canopy cover from the one ha plots were highly correlated to dot-grid woody cover estimates, but most of these areas were in the poor quality areas of the images, hence OBIA cover was not validated with field data. Independent accuracy measures using the dot-grid method correlated well, indicating consistency, and this provided confidence in interpreting results based on these

estimates. The quality of the photographs may have negatively influenced OBIA estimates, because they only covered a single spectral band. Although Floyd and Anderson (1987) stated that vegetation cover is an unbiased estimator of abundance, it was clear from the onset that not all cover was equal (*i.e.*, aerial woody cover versus lateral woody cover). Muchoney and Strahler (2002) found that aerial woody cover always overestimated actual field woody cover. The density, vertical and horizontal profile of woody cover differed for each vegetation community and even within communities in my study (Appendix 5).

Because of the variability in woody cover, which was further compounded by the lack of distinction between trees and shrubs, sable antelope's response to woody cover may have been adversely affected. For instance, sable antelope may avoid areas with high shrub and tree cover because these pose a large predation risk and in another case, they may use areas with high tree cover because of canopy effects on grass quality. The other two hypothetical scenarios, which are likely, are that sable antelope use areas with high tree cover and low shrub cover to maximise foraging on nutritious shade tolerant grass, whilst in the second case, they use areas with low tree and shrub cover as movement corridors. However, these different uses of cover could not be gleaned by using a non-discriminatory measure of woody cover as ecological aspects related to use of woody cover by ungulates were overlooked. For example, Hirth (1977) observed that elk groups at low population densities used areas with more tree cover compared to large groups. Sable antelope may also have preferences in woody cover in the areas they use for foraging, movement, and resting. These requirements can also change in the course of the year, in response to seasonal variation in leaf cover.

The use of a single set of aerial historical photographs limited generalizations from the results since phenological variations affect woody vegetation cover estimates throughout the year. Woody plants respond to soil moisture availability that declines in the course of the year, and this may have had an impact habitat quality (Ogutu and Owen-Smith, 2005). Since the aim of this exploratory study was the identification of underlying habitat use relationships using available data (*i.e.*, aerial photographs and sable antelope locations), a multi-temporal phenological study was not planned. Notwithstanding, an incorporation of these aspects is likely to have led to a balanced study as some of the variation would have been explained.

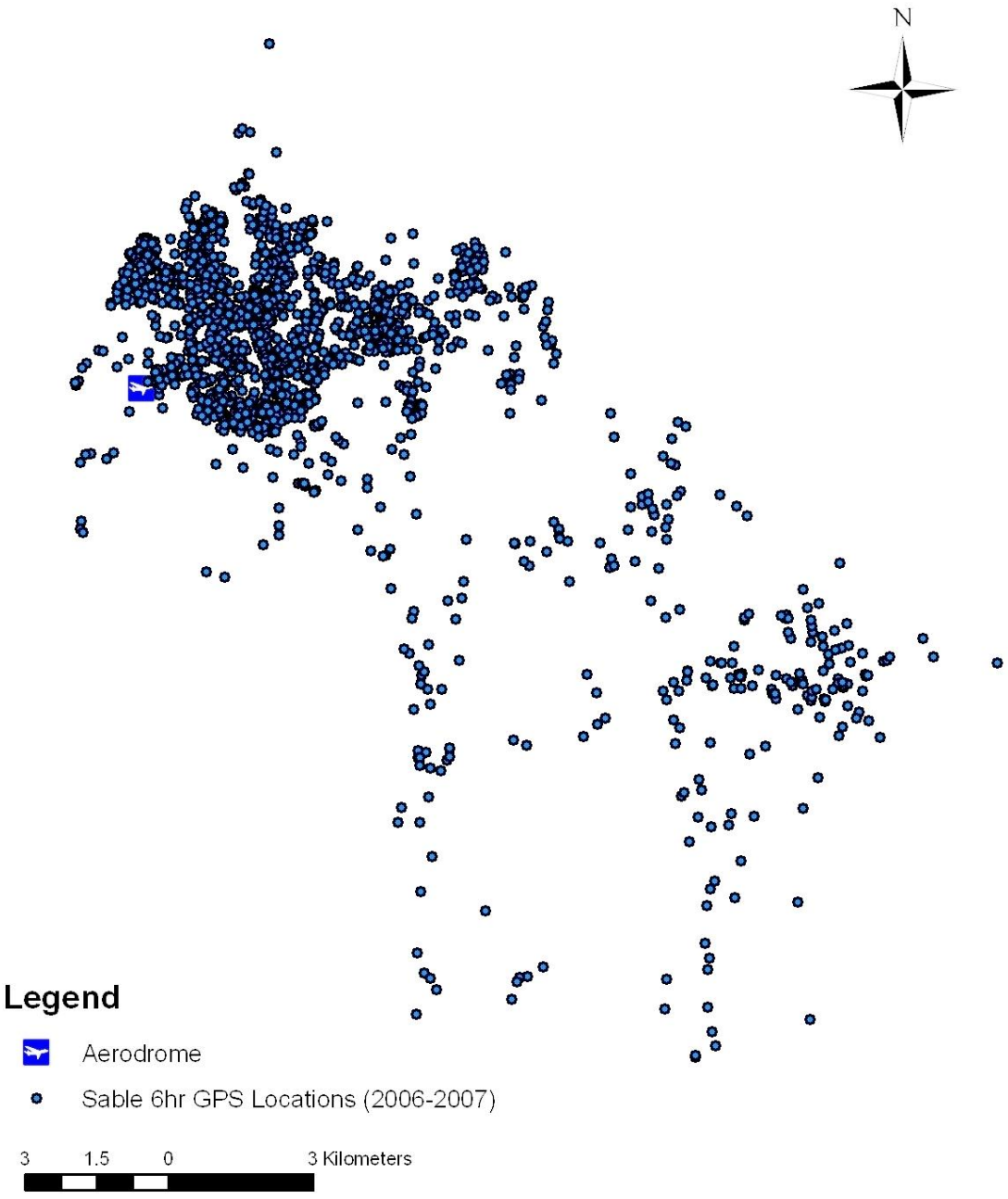
The goal of the study was to investigate the relationships between habitat use by sable antelope and woody cover abundance, and difference in woody cover in use areas. At a 200m spatial resolution, I did not find evidence that sable antelope used habitats with respect to woody cover abundance suggesting that this scale was inappropriate for identifying linear relationships. However, the hypotheses that there are differences in woody cover between and within the seasonal home ranges were supported. There was a significant difference in woody cover between the dry season use areas. Sable antelope used of areas with less woody cover in their home ranges possibly due to anti-predator vigilance/ and or forage maximisation. These results suggest that the management of sable antelope habitat should be done at large scales, which may correspond with the correct spatial scale of resource perception by sable antelope. Larger survey sites (observation plots) in areas with reasonable site occupancies are required for routine monitoring programmes to ensure the survival of sable antelope. Accurate

measurements of habitat elements (*e.g.*, woody cover) are essential for the development of successful RUFs, and the woody cover results from this study suggested that this requirement may not have been fully satisfied.

4.2. Recommendations for further study

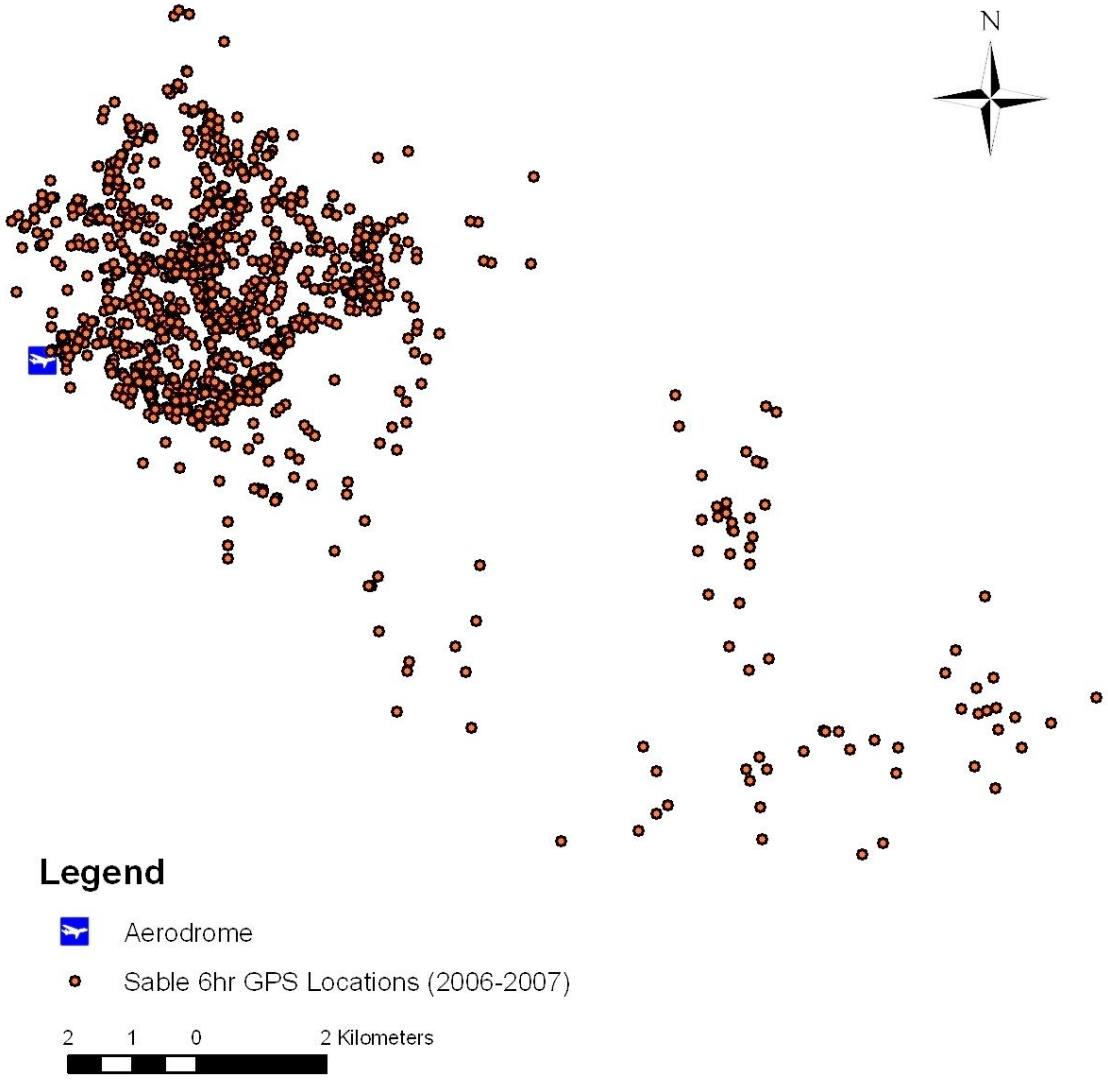
This study provided baseline data in the use of resource utilisation functions in habitat selection by sable antelope in the KNP. However, the lack of woody cover selection by sable antelope at the selected scale necessitates a further study, particularly at increasing scales. In addition, the collaring of more individuals within the same group and adjacent groups may allow for the measurement in *intra* and *inter* herd variation in habitat selection. The collaring of more sable antelope will also enable an investigation into landscape metrics (*e.g.*, patch type, patch shape and size) to be incorporated when investigating habitat use at the landscape level. The delineation of GPS location by time signatures corresponding to animal behaviour (*e.g.*, foraging, resting, and movement) and the use of shorter time sampling intervals will provide specific habitat use data. Also, the integration of UD estimates in site occupancy models will be a useful function to estimate the probability of animal presence. This approach will benefit from the use of high-resolution colour photography and the incorporation of light detection and ranging (Lidar) data, which will enable object based image analysis at fine and coarse scales of the woody cover covariate. A benefit from this approach will be the distinction between trees and shrubs, which was a major limitation in this study.

Appendix 1a



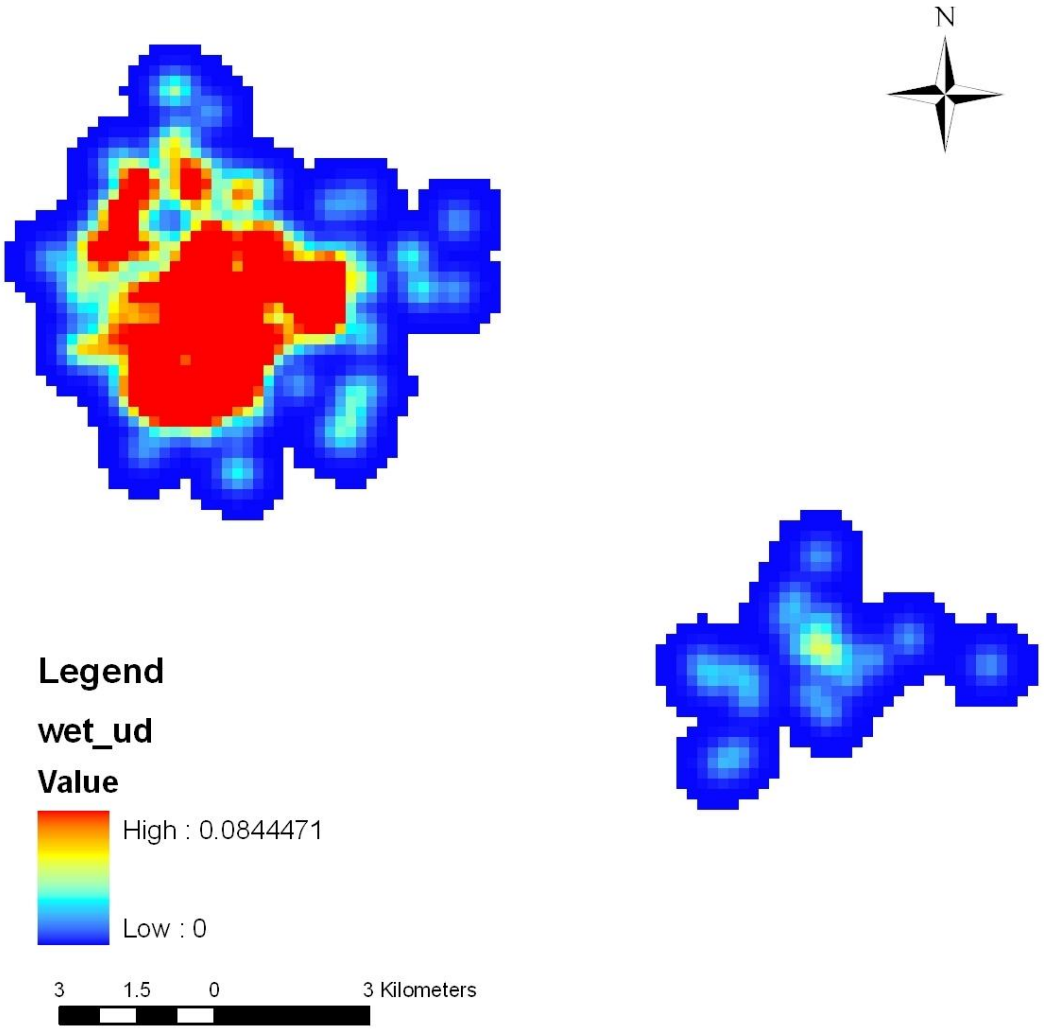
Appendix 1a: Sable antelope 6 hourly GPS locations October 2006 to August 2007

Appendix 1b



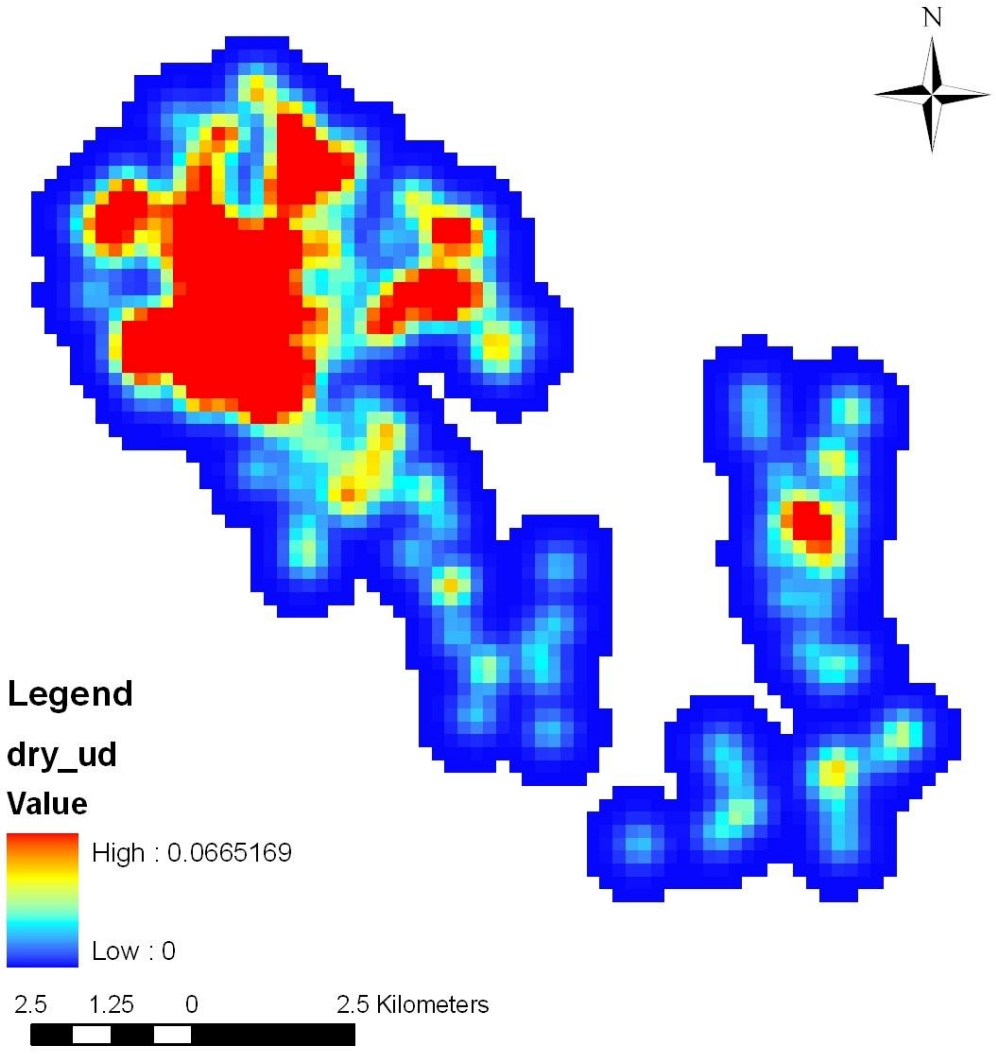
Appendix 1b: Sable antelope 6 hourly GPS locations October 2006 to August 2007 with points leading to the Mphongolo River removed

Appendix 2a



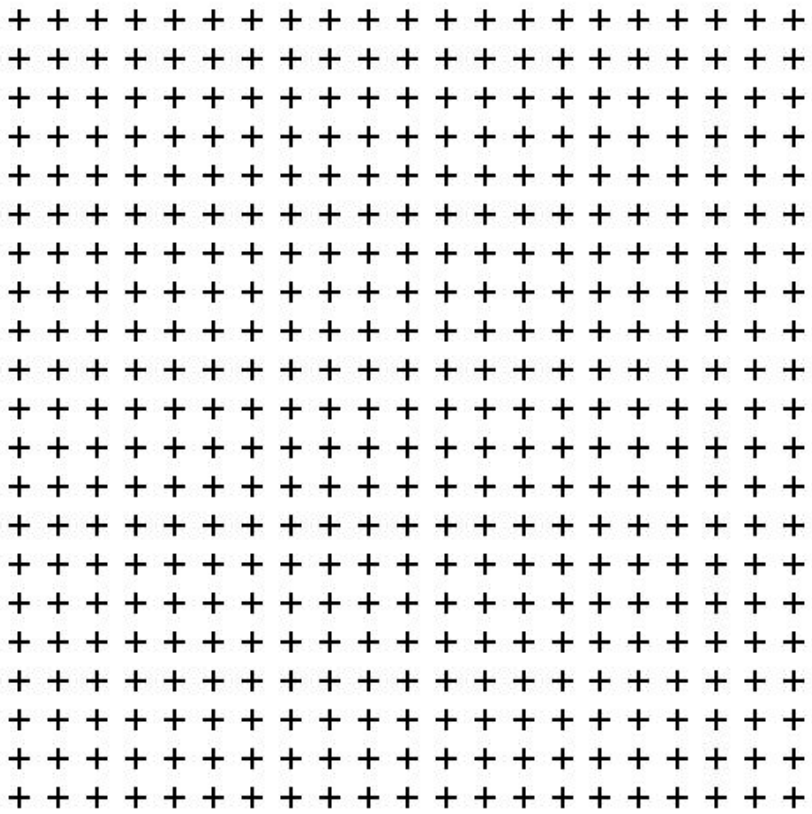
Appendix 2a: Sable antelope wet season (2006-7) kernel density raster, Punda Maria

Appendix 2b



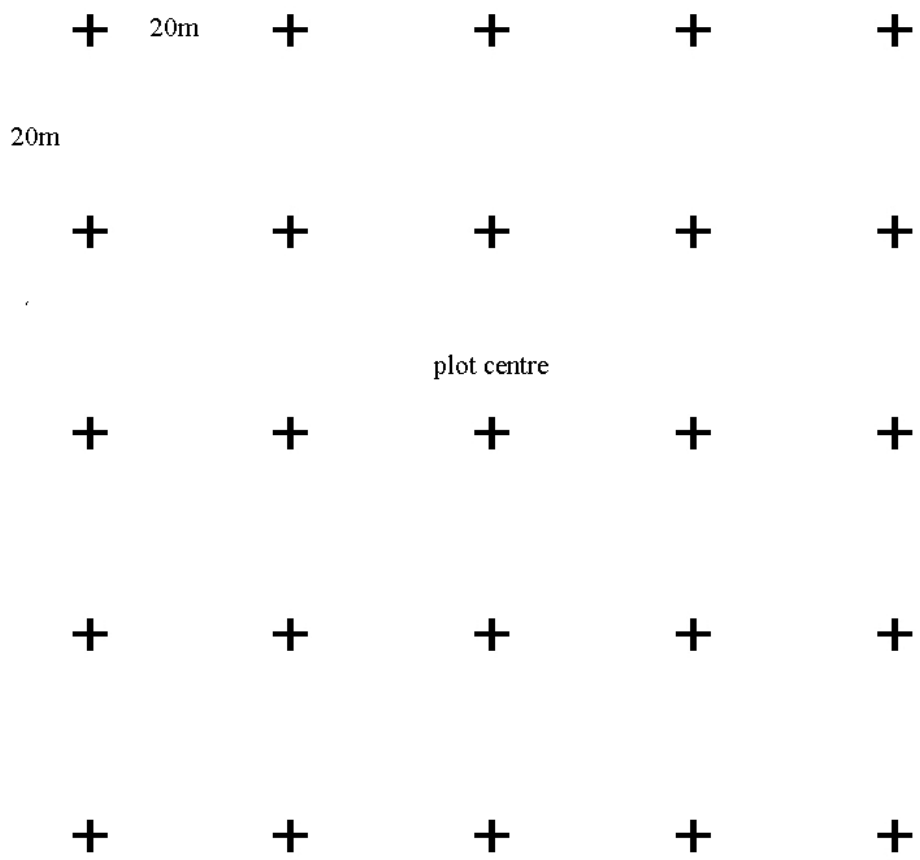
Appendix 2b: Sable antelope dry season (2007) kernel density raster, Punda Maria

Appendix 3



Appendix 3: The regular 10 m x 10 m fine dot-grid cross hairs used for estimating woody cover from digital aerial photographs

Appendix 4



Appendix 4: Field sampling design used for obtaining tree canopy cover from 30 one-hectare plots by taking four reading from a spherical densiometer at the 25 cross hairs

Appendix 5

Appendix 5: Mosaic of different field woody cover configurations in Punda Maria

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